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THE QUARTERLY REVIEW OF BIOLOGY

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CONTENTS

NO. 1, JANUARY, 1926

	PAGE
Foreword	<i>Raymond Pearl</i> 1
The Biology of the Mammalian Testis and Scrotum	<i>Carl R. Moore</i> 4
Symbiosis Among Animals with Special Reference to Termites and Their Intestinal Flagellates.	<i>L. R. Cleveland</i> 51
Experimental Studies on Morphogenesis in the Nervous System.	<i>S. R. Detwiler</i> 61
A Review of the Discovery of Photoperiodism: the Influence of the Length of Daily Light Periods upon the Growth of Plants	<i>K. F. Kellerman</i> 87
Recent Discoveries in the Biology of Atncha.	<i>A. A. Schaeffer</i> 95
New Biological Books:	
Cuénor on Adaptation.	<i>John H. Gerould</i> 119
Brief Notices	124

NO. 2, APRIL, 1926

The Evolution of the Horse. A Record and Its Interpretation.	<i>W. D. Matthew</i> 139
Recent Results Relating to Chromosomes and Genetics	<i>T. H. Morgan</i> 186
The Antiquity and Dispersal of Vascular Plants.	<i>M. L. Fernald</i> 212
Host Resistance and Types of Infections in Trypanosomiasis and Malaria	<i>W. H. Taliaferro</i> 246
Freezing and Survival of Insects at Low Temperatures.	<i>Nellie M. Payne</i> 270
Renner's Studies on the Genetics of Oenothera.	<i>A. H. Sturtevant</i> 283
New Biological Books:	
A Philosophical Interpretation of Nature.	<i>L. J. Henderson</i> 289
Brief Notices	294

NO. 3, JULY, 1926

Abnormal Sexuality in Animals. I. Genotypical.	<i>H. A. E. Crow</i> 315
Human Types.	<i>R. Bennett Bean</i> 360
The Biology of Host-Parasite Relationships Among Protozoa Living in Man	<i>Robert W. Hegner</i> 393
The Maturation Divisions in Relation to the Segregation of Homologous Chromosomes.	<i>E. Eleanor Carothers</i> 419
Eleven Thousand Generations of Paramecium.	<i>Loranda L. Woodruff</i> 436
New Biological Books:	
A New Word for an Old Thing.	<i>William Merton Wheeler</i> 439
Brief Notices	444

No. 4, OCTOBER, 1926

PAGE

Fetal Growth of Man and Other Primates.....	<i>Adolph H. Schultz</i>	465
The Biology of the Termite Castes.....	<i>Thomas Elliott Snyder</i>	521
Age and Area.....	<i>J. C. Willis</i>	553
The Productivity of Lakes.....	<i>A. Brooker Klugh</i>	572
New Biological Books:		
A Static Theory of Heredity.....	<i>Julian Huxley</i>	580
Brief Notices.....		584
The Cost of Biological Books in 1926.....	<i>Raymond Pearl</i>	606
Index to Volume I		619

THE QUARTERLY REVIEW *of* BIOLOGY

FOREWORD

IT IS reported that there exist in the world today approximately 25,000 reputable scientific journals, devoted in whole or part to the publication of the results of research. In the face of such an overwhelming statistic it is entirely appropriate to raise the question: Why start another? As THE QUARTERLY REVIEW OF BIOLOGY stands, at the moment, in the position of the latest addition to the already large population of scientific journals, there is an obligation to make some statement as to its *raison d'être*. This obligation may fairly be judged a moral one, because, like all forms of population growth, that of scientific journalism shows definitely a tendency to approach a state of troublesome saturation. It has already become a physical impossibility for any person, professional or lay, to read carefully and critically in its original form the whole of the published output of new results of research work in any general field of science, such as chemistry, physics, biology, etc., even if he attempted to do nothing else. The same thing is indeed true of all the special fields of science except the narrowest.

At the same time it is apparent to the philosophically minded person that one of the most significant trends of science in the twentieth century is its integrative tendency. No science is any longer regarded, by even the narrowest specialist, as sufficient to itself. Biology cannot advance completely separated from physics, chemistry, and mathematics. The biologist who expects to deal with his problems in any degree of penetration, has got to know a good deal of these other subjects, and this knowledge in the long run has got to be something more than the elementary text book sort. Similarly, how far can an astronomer expect to get today without being a good deal of a physicist, or a physicist without being a mathematician, or a physiologist without being a chemist? This tendency may be interpreted to make a somewhat belated recognition on the part of Science that Nature is itself a highly integrated piece of business, of almost infinite complexity. When one starts to take it apart and put it together again, to the end of seeing how it works, he will be simply showing ordinary common sense if he has in his working tool kit as many different kinds

of wrenches, chisels, hammers, yardsticks, etc., as possible.

These two tendencies, the ever-increasing output of highly technical results, on the one hand, and the ever-increasing necessity for the successful researcher to know a good deal about other fields of science than his own specialty, on the other hand, are patently antagonistic. Something has got to be done to bring about an effective working compromise between them. One highly important step in this direction is the development of abstract journals. This development has reached a high pinnacle of success in this country in the field of chemistry, where, in *Chemical Abstracts*, we have a model journal of its type. There is every reason to hope and to believe that *Biological Abstracts*, under the aegis of the National Research Council, will be equally successful in its field.

While abstract journals are a vital necessity to the progress of science, and are to be in every way encouraged and still further developed, they do not wholly solve the problem. There are two reasons why they do not. In the first place they tend themselves to become so large, in spite of every conceivable mechanical condensation in the way of abbreviation and the like, that no one can read them *in toto*. In the second place, in spite of the cleverest classification, arrangement, and indexing of the material, abstract journals necessarily lack in significant degree the qualities of coördination and integration. They present to the enquiring reader a vast assemblage of trees but no adequate picture of the forest. But it is precisely picture maps of the various developing forests of science that we most need if we are not to go wholly mad, and see our civilization perish because all the persons capable, by genetic endowment, of leading it, are confined

in asylums as the result of a hopeless confusion of ideas.

THE QUARTERLY REVIEW OF BIOLOGY, with becoming modesty but nevertheless courageous mien, steps forward to do its bit towards postponing or perhaps altogether averting such a devastating catastrophe. It will offer to the reader authoritative and comprehensive reviews of the present state of knowledge in the different fields of general biology. The articles will be written by specialists, who alone are capable of giving accurate, balanced and critical summaries of the present position in various lines of inquiry. The first function of THE QUARTERLY REVIEW OF BIOLOGY will be to help the man of science, whether biologist, chemist, astronomer, or devotee of any other *Fach*, to keep soundly oriented as to the general progress of biology.

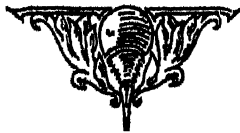
It is hoped that it may also serve usefully another group of readers. There is a marked recrudescence just now of the age-old warfare between religion and science. Some of our scientific *confrères* appear either to have forgotten, or never to have grasped, the significance of the length and bitterness of the struggle which finally freed the human mind from the shackles imposed and maintained through centuries by organized religion. They go about plaintively bleating that there is no conflict between science and religion, to the great joy of the shrewder fundamentalists, who perceive at once the enormous aid which such views will be to them in their work of forging again the fetters from which Huxley finally freed human-kind. The plain fact, of course, is that there can never be any real compromise between science and mysticism, between the real and the supernatural, between light and darkness, between the demonstrable, verifiable truth which

makes us free and ancient superstitions grounded in phallic folk-lore.

The experience of centuries indicates that there is only one way effectively to meet the menace of Fundamentalism, which in a real sense threatens the continuance of those elements in our civilization which every intelligent man holds dear. It is by the diffusion of scientific knowledge. Man's emancipation from the domination of priesthoods of one brand or another has been in precise proportion to the depth and breadth of the understanding of nature which science has given him. We hope that *THE QUARTERLY REVIEW OF BIOLOGY* may help in the diffusion of a sound knowledge about biological matters among intelligent men and women who are not professionally scientific workers. No at-

tempt will be made to attain this end by the method of writing down to the supposed intellectual level of a lay audience. Popular scientific writing which takes as its target a mental age of about ten, is, we believe, quite as nauseating to intelligent lay readers as it is to men of science. But we think that there exists in this country a fairly numerous body of cultivated men and women who are genuinely interested in knowing about the progress which biology is making, and quite as capable of understanding a clearly written and logically ordered presentation of it, as is the average physicist or chemist, or indeed the specialist in biology itself who cultivates a field remote from the particular one under discussion. To this group also we offer *THE QUARTERLY REVIEW OF BIOLOGY*.

RAYMOND PEARL.





THE BIOLOGY OF THE MAMMALIAN TESTIS AND SCROTUM

By CARL R. MOORE

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IN DEALING with some phases of the biology of the mammalian testis a limited discussion may follow two major lines of interest: (1) a consideration of certain influences on the germinal portion of the organ—spermatogenesis—and (2) a brief discussion of the testis as an organ of internal secretion. The products of these two testicular functions have at times been referred to respectively as the external and internal secretions; the study of spermatogenesis is the older and perhaps better understood of the two, but recent study has largely concerned itself with internal secretions, almost to the exclusion of the primary function of germ cell production. We shall consider first some of the general conditions that influence the production of germ cells, particularly the functional significance of the scrotum; secondly, the internal secretory function will receive our attention.

I. GENERAL CONSIDERATIONS

The testes of most mammals are located outside the body cavity in a pouch, or scrotum, embryologically a derivative of the peritoneal cavity. A duct, the ductus (vas) deferens leads away from the epididymis to convey spermatozoa to the exterior. Embryologically, the testes arise from the genital ridge of the urino-genital fold high up in the body cavity (2) (6), and are fundamentally, therefore, organs of the abdomen; they remain so in

all vertebrate classes except mammalia. In this group a new condition has made its appearance in that the testes, though arising near the kidneys, become progressively displaced posteriorly and in the majority come finally to be located in the scrotum (before birth in man). In some mammals (rodents, etc.) the pathway of descent remains open throughout life, but in man and most mammals the inguinal canals become closed.

The factors involved in the backward regression of the testis, both phylogenetically and ontogenetically, are not entirely clear. Embryologically a cordlike ligament, the gubernaculum (Hunter), exists between the developing testis and the anterior abdominal wall, and it is supposed by some anatomists (42) that muscular fibers of the gubernaculum exert a continuous pull on the testes toward the anterior abdominal wall while others (6) believe that the principle of unequal growth of the body in comparison with the fibrous cord will explain the backward regression of the testis in ontogenetic development.

Too little attention, perhaps, has been given to the exceptional formation of the scrotum in mammals. Its significance or function has been lightly touched until recently and a few enlightening facts may give us a new conception of this relatively recently acquired structure. Herbert Spencer (173) in discussing the general principles of biology speaks of the

peculiar condition found in mammals in the following terms:

But now let it be confessed that all phenomena of organic evolution must fall within the lines above indicated, there remain many unsolved problems. Take as an instance the descent of the testes in mammalia. Neither direct or indirect equilibration accounts for this. We cannot consider it an adaptive change, since there seems no way in which the production of sperm cells, internally carried on in the bird, is made external by adjustment to the changed requirements of mammalian life. Nor can we ascribe it to survival of the fittest; for it is incredible that any mammal was ever advantaged in the struggle for life by this changed position of these organs. Contrariwise the removal of them from a place of safety to a place of danger would seem to be negatived by natural selection. Nor can we regard the transposition as a concomitant of re-equilibration since it can hardly be due to some change in the general physiological balance (page 575).

The monotremes, most edentates, sire-nians, cetaceans, some proboscidi-ans, and seals among carnivores possess complete or nearly complete abdominal testes (209). In many edentates and rodents the testes may be abdominal for the majority of the year but temporarily descend during the breeding period; this is essentially true in the Chiroptera. The majority of ungulates, carnivores, and all primates have a scrotum, and closure of the inguinal canals separates the testes from the abdomen. In seasonal breeding animals the testes are usually abdominal until the approach of rut when the testes become enlarged and reside in the scrotum.

In general it appears that an evolution of the scrotal condition has occurred and Wiedersheim (209) states "originally, the descent of the testes did not occur until sexual maturity in all cases, but in many mammals (e.g., marsupials, ungulates, carnivores, primates) the process has gradually become shifted backward ontogenetically to earlier periods, so that the formation of the scrotum takes place independently in the embryo in the form

of the external genital folds. . . ."

Cunningham (43) discussing its occurrence, evolution and significance remarks "Various causes have been suggested for the formation of the scrotum, but no one has even been able to suggest a use for it. It has always been quite impossible to bring it within the scope of the theory of natural selection. The evolution of it can only be explained either on the theory of mutation or some Lamarckian hypothesis" (page 147). In his further remarks Cunningham removes it from the possibility of having arisen through mutation and supports the Lamarckian hypothesis put forward by Woodland (112) in 1903. Woodland states

I hold that, in the majority of the mammalia, the testis attachment has throughout the history of the race been constantly subjected to severe strains consequent on the character and conditions of mammalian locomotion, and that on account of the resulting disruption or distention of the mesorchium, the testis has migrated in a postero-ventral line (i.e., in an opposite direction to the forward and upward accelerations imparted) coming to lie at the terminal periphery of the body wall and forming the scrotal protrusion. Just as when a man runs, a weight in his coat-pocket will periodically drag and ultimately wear a hole in the lining by constant distention, so the testis of mammals has responded to like forces resulting in descent (page 325).

Speculations on the mechanistic procedures and forces employed, are perhaps less fruitful than have been some of the more recent enquiries into its possible function, since the former conception is excluded from, but the latter aspect subject to, experimental analyses. Can we therefore offer any approach to a functional analysis of this structure which Cunningham stated a few years ago had never been attempted?

Recent work in this laboratory (121, 122, 123, 125, 128, 131) we believe has proved that in the higher mammals *the scrotum is a structure whose function is the*

maintenance of proper temperatures for the testes to carry on the differentiation of germ cells; it is an essential thermoregulator for the testes and higher mammals are incapable of producing spermatozoa without such a regulatory control provided by the scrotum. For descriptive purposes a bit of general histology is necessary.

Figure 1 is a portion of a cross section through a rabbit testis; though used for an experiment it shows normal seminiferous tubules in cross section. The *germinal epithelium* composed of spermatogonia, spermatocytes, spermatids and spermatozoa represents a typical condition for all mammals; spermatozoa may be seen projecting into the lumen of the tubules. Between the seminiferous tubules can be seen a small amount of connective tissue among which are a few larger cells; these are the *interstitial cells* or cells of Leydig (86) considered by many workers as the source of the internal secretion of the testis. These will be

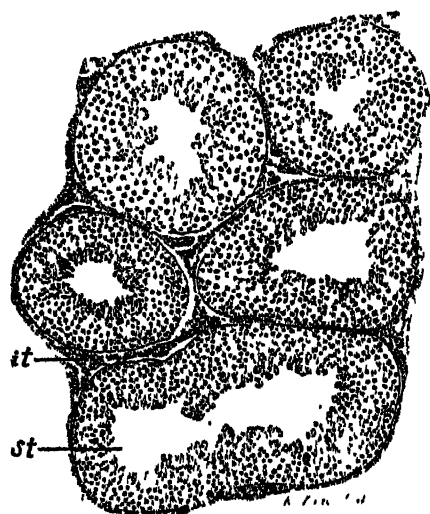


FIG. 1. SECTION THROUGH CENTER OF RABBIT TESTIS SIX MONTHS AFTER VASOLIGATION (LEFT TESTIS OF FIGURE 6, B)

st, normal seminiferous tubules, it, interstitial tissue

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II. CRYPTORCHIDISM

Sometimes the testes of man and higher mammals are not to be found in their normal scrotal position; having failed to descend they may be located in the abdomen or in the inguinal canal and are hidden or cryptorchid (for structural condition see figs. 4 and 5). The condition has long been known but the oldest account to which I have made reference is that of John Hunter, that very keen anatomist of the 18th century. Hunter (75) in a lecture given in 1756 discussed the site of origin of the testis of mammals in the abdomen, and the gradual descent of these into the scrotum in the human foetus at about the eighth month of foetal life. He realized the occasional imperfection due to failure of descent. "Sometimes in the human body, and in many other animals, and very often in sheep, the testes do not descend from the cavity of the abdomen till late in life, or never at all." He suspected that the cause for this failure to descend "Originates in the testicles themselves." Their condition was also partly appreciated for "When one or both testicles remain through life in the belly, I believe that they are exceedingly imperfect, and probably incapable of performing their natural functions, and that this imperfection prevents the disposition for descent from taking place" (page 56).

Goubaux and Pollin (57) studying testes retained in the abdomen in man, sheep, horse, pig and dog stated that usually the abdominal testis was both less voluminous and lighter in weight than the scrotal testis on the opposite side. These writers stated that abdominal testes did not produce spermatozoa and that retention of both testes rendered an animal sterile. Godard (54) determined that seminal fluids from men with both

contain spermatozoa, nor did cadaver cryptorchid testes show spermatozoa. Monod and Arthaud (111) studying the abdominal testes removed from man were of the opinion that younger individuals retained a diminished capacity of producing spermatozoa. Individuals of later life however were rendered sterile from traumatic influences and resulting sclerosis of the organs. In the end all ectopic testes were, according to them, deprived of their spermatozoon producing capacities. Griffiths (59) pointed out that testes of the dog and man retained in the abdomen or in the inguinal canal were degenerate so far as sperm production is concerned. In those testes located intermediate between the abdomen and scrotum the seminiferous tubules were devoid of germinal epithelium. He emphasized the necessity for the testis to completely descend into the bottom of the scrotum before they can carry on their gametogenetic function. Regaud and Policard (149) called attention to the lack of germinal tissue in the undescended testis of the pig and mention particularly the considerable apparent increase in interstitial tissue.

Some of the most exhaustive work on undescended testes in the human is that of Felizet and Branca (45, 46). These investigators studied a series of abdominal testes from six year old boys to adults and point out that seminiferous tubules are the characteristically affected portions of the gland, the epididymis remaining normal in structure. In ectopic testes removed from a preadolescent individual the single layered undifferentiated germinal epithelium differed but little from that of similar aged normal testes. As the period for the differentiation of spermatogonia, spermatocytes and spermatids approaches, degeneration follows and the epithelium never reaches the completely

differentiated stage. Whereas later writers, and some earlier ones, believed cryptorchid tests at puberty did reach and maintain spermatozoon differentiation for a short time, Felizet and Branca were unable to find a single case among the fifty-one studied where this appeared true. Of this number they report sixteen cases with spermatogonia present; twelve cases with differentiation to the spermatocyte stage, and only two cases, of the fifty-one, showing spermatids: no cases with spermatozoa present were found. The interstitial tissue was usually more abundant in normal testes but the number of Leydig cells varied considerably.

Bouin and Ancel (22) studied ectopic testes of the boar and dog and noted in all cases that the seminiferous tubules were smaller in caliber, and contained only the cells of Sertoli; the interstitial cells were usually abundant. Corner (40) studied histologically sixteen cases of ectopic testes removed from man but did not find evidences of spermatogenesis in any case. Whitehead (205) similarly found that an undescended testis of the horse was degenerate so far as the germinal tissue is concerned. Hanes (65) studied fifty-six undescended testes from the pig, seven from the sheep, and six from man. He states that in no case was spermatogenesis in progress and the tubules contained only Sertoli cells; the intertubular spaces were well filled with masses of Leydig cells. Bland-Sutton (20) studied histologically the ectopic testes removed in the course of twenty-five years surgical work (number not given) and mentioned that only one contained spermatozoa. He believes that ectopic testes develop to their normal differentiated condition at puberty and retain the capacity to produce germ cells for a year or two. His opinion however, receives but little support from the studies of most investigators but it may be men-

tioned here that Moore (122) studying experimental displacement of the guinea pig testis found that such an organ retained in the inguinal canal with one pole projecting into the upper portion of the scrotum might produce normal germ cells in one part and not in another. It is possible that the single case bearing spermatozoa reported by Bland-Sutton was a low inguinal canal retention instead of an abdominal one. Goddard (55) studied five cases of the retained testis removed from men 19 to 25 years and in no case was there any indication of spermatogenesis, though the interstitial cells were well preserved and apparently present in an overabundance.

What to do with an undescended testis is a problem that ever confronts the surgeon, and because the fundamental conditions of the gland and its potentialities have not been understood there have been many opinions voiced and different procedures employed. Even in Hunter's period (1756), and purely on philosophical grounds, he argued that nature should be assisted in all ways possible to bring the testis into its normal locality in the scrotum. Later the idea that an ectopic testis is decidedly prone to develop neoplasms and metastasize became more or less prevalent and tended to encourage removal of such organs. The knowledge that an ectopic testis can still exert its internal secretory function, however, has led many to remove the organ from the inguinal canal, in order to cure or lessen the tendency to hernial formation, and allow it to remain in the abdomen. Thus Corner in 1904 reviews the general question of the value of an incompletely descended organ and recommends replacing it in the abdomen. He believes it useless to attempt a scrotal return and considers the testis of no use except as an organ to produce sex hormones. Bland-

Sutton likewise, believing the ectopic organ useless, exercises but little care in its preservation. He and others, believe the organ was retained in the abdomen because it was intrinsically defective. Keyes and MacKenzie (78) on the other hand advise an operation to place the undescended testis in its normal scrotal position before the stage of puberty, thinking, evidently, that a mere possibility remained for it to develop into a functional condition. Bevan (18) describes a technic for restoring the ectopic testis to its position in the scrotum and advises this operation.

The advocacy of the operation on the human individual, however, is from the very nature of the case difficult to determine. Furthermore since the real fundamental condition of, or the potentialities of, an abdominal testis have not been understood a rational basis for procedures has not been clearly indicated. The question of why a testis is found in the condition of degeneration in over ninety-nine per cent of all reported cases should be settled. Of necessity this involves animal experimentation and it is from this field that many new facts have been derived.

Up to about the year 1890 three different conceptions had been advanced to explain the condition of naturally occurring cryptorchid testes: (a) It was believed by some that the abnormal condition was due to an imperfect embryological development and that its structure rested primarily upon the faulty formation of the organ. (b) Some authors held that early development was normal, but differentiation of the germinal products failed to pass beyond an embryonic stage of the germinal epithelium. (c) Others believed that the testes acquired the capacity to produce spermatozoa, retaining same for a year or so, but on account of the abnormal position occupied regression takes place and leaves

the organ deprived of its germinal tissue.

The English anatomist Joseph Griffiths (58) is to my knowledge the first individual to attempt a solution of the problem by experiment. In 1893, working with the dog, he demonstrated that a testicle of a puppy that had descended normally into the scrotum would never produce spermatozoa if it was returned to the abdomen by an operation, despite the fact that its vas deferens, blood supply and nerve connections were entirely normal. Such a testis developed but little farther than the embryonic stage of differentiation; the opposite scrotal testis differentiated normally. The testis of an adult dog, actively producing spermatozoa, would within a few months after having been replaced within the abdomen, show a condition similar in all respects to abdominal testes; all the germinal tissue vanished and only the single layer of Sertoli cells remained. He proved therefore that the structural condition of an ectopic testis was not due to any inherent defect within the organ but was a function of its abnormal environment. Some influence from its location was responsible for its condition and he speculates at some length on the situation. "What, then, can be the reason that in some, a limited number of animals, the scrotal position is essential to structure and function? . . . can it be that the very turbulence of this region is requisite for its perfect development and the maintenance of its functions in certain animals? . . . So far as I am aware, no satisfactory answer has ever been offered to this most interesting question" (pp. 496-497). Though not able to determine the active influences brought to bear upon the testis in its abnormal location Griffiths' tendency was distinctly directed to the scrotal relationships as a solution. He emphasized the necessity of

the testis descending completely to the bottom of the scrotum before it could exercise its normal functions, and furthermore compared the condition of the testis of seasonal hibernating mammals with the abdominally retained testis of scrotal animals.

The Danish investigator Knud Sand (160) utilized the method of Griffiths in replacing the normally descended and actively functioning adult testes of rats and guinea pigs into the abdomen. His study, however, did not advance our knowledge of the problem of the degenerate testis when it is located in a strange environment, for his chief interest lay in the behavior of the interstitial tissue which he believes becomes greatly increased. He confirmed Griffiths' statements that normally functioning adult testes when replaced in the abdomen are converted into typical ectopic testes within a few months; the germinal epithelium that was actively producing germ cells at the time of elevation had all disappeared within the course of three months with only the single layer of Sertoli cells remaining.

This problem along with many others was being studied in this laboratory in 1921 (Moore 118). An attempt was being made to determine the real causes of the degeneration of the testis when placed in the abdomen. By experiment such possibilities had been eliminated as infection, physical connections with some part of the scrotum, abnormal pressures, and disturbance of blood or nerve supply and it was stated that a differential body temperature was probably the causal factor in degeneration; experiments testing this hypothesis, though under way, were incomplete.

Crew (41) purely on hypothetical grounds suggested that the cause of the lack of spermatozoa in the imperfectly

descended testis might be due to a higher temperature in the abdomen than in the scrotum, considering that it was this higher temperature that might be responsible for the non-appearance of an active epithelium. He thus was the first with a suggestion that has proven in our laboratory to be the causal factor in the structural condition of a testis either never having descended from the abdomen, or having descended and accomplished its complete differentiation reverts to the typical ectopic type when by experiment it is returned to the abdomen.

Moore (122) reporting more in detail

number of tubules contain only degenerate cells and a mass of debris. Somewhat later than the sixth day after elevation the tubules may have sloughed the major portion of the germinal epithelium and the remaining cells may have coalesced into multinucleate protoplasmic masses or "Giant Cells" (see fig. 3). By twenty days practically all the former active germinal epithelium was absent; Sertoli cells and a few spermatogonia remained. The interstitial cell mass appeared progressively more conspicuous, but the significance of these will be dealt with more in detail in section IX.

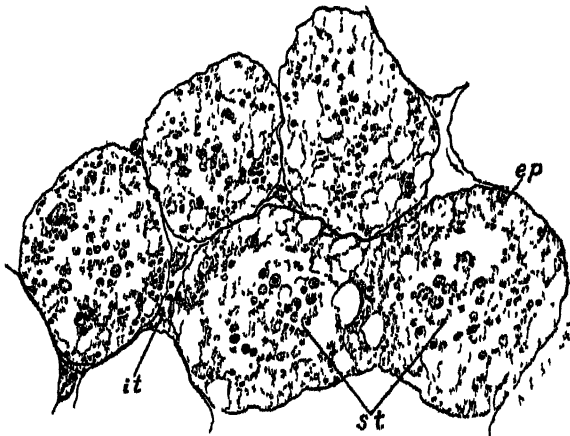


FIG. 2. SEMINIFEROUS TUBULES OF ADULT GUINEA-PIG TESTIS SHOWING DIMINUTION SEVEN DAYS AFTER ELEVATION TO ABDOMEN

p, degenerate epithelial wall; *st*, interstitial tissue, *st*, seminiferous tubules with degenerating cells in lumen

on the observations made with experimentally produced cryptorchid testes found that a normal adult functioning testis of the guinea pig shows decided degeneration of the germinal epithelium within six days after being elevated from the scrotum to the abdomen (see fig. 2). This degeneration is noticeable from the fact that the seminiferous tubules are disorganized, and many loosened cells occupy the lumen filling the latter with discrete cells some of which are normal and others fragmented; a considerable

So long as the testis remained in the abdomen it continued degenerate; followed for longer than a year the organ as a whole progressively diminishes in size and the seminiferous tubules shrink to one-fourth or one-fifth their normal diameter. If, however, the testis in a partial descent into the scrotum was held within the inguinal canal with its lowermost end projecting into the upper portion of the scrotum there might be found one portion in which the tubules could still carry on their gametogenetic function, though ap-

parently in a diminished capacity, while another portion located more closely to the interior of the abdomen was entirely degenerate.

It was desirable to learn more of the potentialities, of such a degenerate testis, and to determine if it retained the capability of regenerating into a normal functioning gland. Moore determined that recovery did occur if the testis was replaced in the scrotum. Twenty-four days

It would appear therefore that the surgeon should take especial care to see that ectopic testes are restored to their normal environment. Their degenerate condition, while it may be so, is not necessarily due to faulty embryological formation. Davis (44) has recently enumerated as causes for lack of scrotal descent (1) defects in the mesorchium, (2) paralysis, absence, or faulty insertion of the gubernaculum, (3) narrowness of the vaginal

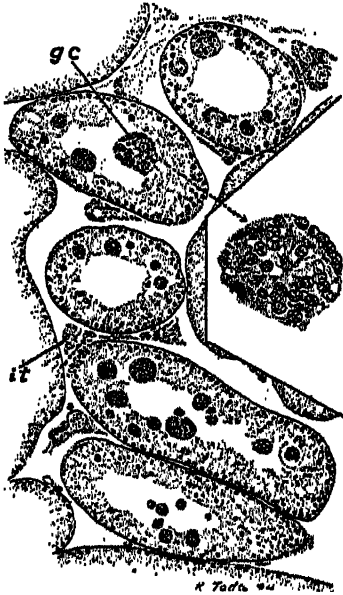


FIG. 3. TUBULES OF ADULT GUINEA-PIG TESTIS CONFINED TO ABDOMEN THIRTEEN DAYS

gc, multinucleate giant cells formed from coalescing germinal cells

abdominal retention reduced seminiferous tubules to a single layer of cells among which were a few spermatogonia; return of such testes to the scrotum led, within three months, to testes with normal tubules and quantities of spermatozoa. Thus it is seen that the testis must reside in the scrotum to be able to carry on its function of gametogenesis but the limits of degeneration with recovery still possible have not yet been determined.

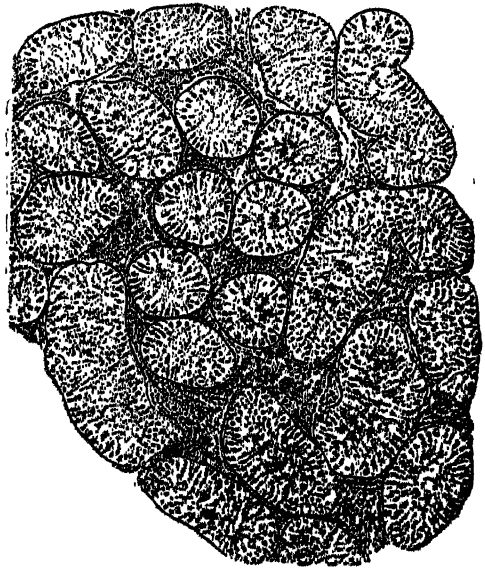


FIG. 4. SEMINIFEROUS TUBULES FROM UNDESCENDED TESTIS OF AN ADULT DOG

process, or large size of the testicle, (4) shortness of the spermatic cord, (5) rudimentary or obliterated scrotum, and (6) premature obliteration of the inguinal canal. It seems probable that placing the testis in the scrotum by operation would lead to its normal development in such cases. Operation before puberty certainly carries many strong chances that a child with doubly undescended testes may be given the chance of acquiring his normal germ cell production capacity by a small operation, whereas without it there is no

chance of his acquiring this function. How long after puberty a testis returned by operation to the scrotum can regenerate into a normal organ has not yet been determined.

In addition to studying experimental cryptorchidism in the guinea pig we have performed similar experiments on rats, rabbits and sheep. Thus Moore and Oslund (131) determined that a normal breeding ram testis removed from the scrotum and replaced in the abdomen surrounded by all its natural coverings, with blood supply, nerve connections and vas deferens in a normal condition, would be

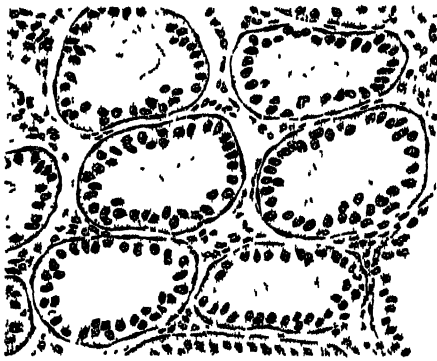


FIG. 5. SEMINIFEROUS TUBULES FROM TESTIS OF ADULT RAM REMOVED FROM SCROTUM TO ABDOMEN FOR THREE MONTHS

rapidly converted into a degenerate testis with a single layer of Sertoli cells in the seminiferous tubules (see figs. 4 and 5) Moore and Quick (129) obtained similar results in the rabbit. In the rat (Moore, details unpublished) degeneration follows in the testis, elevated and confined in the abdomen, but the degree of degeneration is by no means so pronounced as that in the guinea pig, sheep and rabbit. A rat testis confined to the abdomen for a period of six months is considerably degenerate and no tubules of a normal character can be found, but they are more nearly normal than a guinea pig testis similarly retained

for fifteen days. It appears that the rat testis can tolerate greater ranges of temperature than can the guinea pig testis. This may be accounted for by supposing that the rat testis is not so dependent upon a finely graded regulation of its environment as is the testis of the guinea pig and consequently represents a lower grade of differentiation as regards the scrotum (see section V).

III. VASECTOMY

The problem of vasectomy, or vasotomy, by which is meant the production of an interruption in the course of the ductus or vas deferens, has been one of the most confused problems relating to the testis. Popularized it is known as the Steinach operation for rejuvenation; it has served at the same time as a theme for popular fiction and in the hands of the surgeon as a supposed efficacious method of treatment for many ills of human individuals.

One of the earlier observations on the effects of occluding the vas deferens is that of Sir Astley Cooper (39). He ligated one vas deferens in a dog, and on the opposite side ligated the artery and vein without interfering with the vas deferens. The testis whose artery and vein were ligated "gangrened and sloughed." Operated in 1823 the dog was kept until killed in 1829. During six years it was noted in coitus two separate times but no issue followed. Observed after killing, the testis with its epididymis was notably increased in size and the latter, with the short stub of appended vas deferens, was gorged with spermatozoa. Occlusion of the duct had been complete and the two ends of the severed duct were separate. This conclusive experiment showed without doubt that merely closing the outlet duct of the testis had no effect upon the germinal portion of the organ;

spermatogenesis continued for six years after operation and the epididymis became much enlarged to accommodate the products of germinal cell activity.

Gosselin (56) some years later dissected human cadavers and noted cases in which the vas deferens was entirely occluded, and had been undoubtedly for years, but the enlarged epididymis contained quantities of spermatozoa. Brissaud (29) and Griffiths (61) with rabbits and dogs respectively found that occlusion of the outlet duct had no influence on spermatogenesis. Griffiths (62) a year later, however, determined that testes of the dog rapidly lost the germinal portion if blood vessels passing to the testis were injured. Simmonds (170) in human autopsies found occlusion of the vas deferens of years standing without any injury to the generative portion. Neither testicular degeneration nor loss of the germinal epithelium had occurred and the epididymis was enlarged from the immense amount of spermatozoa carried to it.

Thus in man, dogs and rabbits it was well established by incontrovertible data before 1900 that blocking the outlet duct from the testis had no effect in causing the testis to become aspermatic. Gametogenesis continued for years and quantities of spermatozoa were to be found in the epididymis and the proximal portion of the vas deferens.

About 1903 when results on experimental studies of the testis became more numerous contrary results began to appear. Richon and Jeandelize (156) stated that rabbit testes, whose vas deferens had been experimentally occluded contained no spermatozoa, and that the seminiferous tubules were degenerate. The extensive study of sex glands conducted by Bouin and Ancel, however, was the chief factor in changing the tide of opinion relating to the effect of vas deferens occlusion. Summarizing

many of their different studies Bouin and Ancel declare that closing the outlet from the testis, by ligation and resection of a portion of the ductus deferens, invariably leads to degeneration of the germinal tissues of the testis. They worked with guinea pigs, dogs and rabbits, young and adult. According to their account ligation of the outlet duct before the stage of puberty does not interfere with the attainment of complete germ cell differentiation, but after this attainment the seminiferous tubules rapidly lose their lining epithelium and become converted into a testis entirely similar to the cryptorchid testes found in nature. They dismiss the contrary findings of the earlier writers by assuming an insufficient length of time after operation before the animals were killed. It should be remembered that Cooper's dog was not killed until six years after the operation for closure of the tube, and pathological occlusion in man had been present for years without testis degeneration. The question at issue is not whether Bouin and Ancel obtained degeneration of the germinal epithelium after vas deferens ligation, for undoubtedly they did; the real question is whether the degeneration they saw was due to the occlusion of the duct or whether factors not necessarily related to this operation are the real causes.

Shattock and Seligman (169) performed double vasotomy on Herdwick rams, but despite the fact of double, complete vas deferens occlusion for eighteen months the testes were normal in size and spermatogenesis continued; the epididymis was much larger than normal due to the retention of the products of spermatogenesis and consequent distension of the epididymis. They note that testes may be abnormal if the blood vessels had been included in the ligature of the vas deferens.

Wallace (198) reviews the results of vas deferens ligation in man. Sometime before this period it was an accepted surgical practice, due to the suggestion of earlier workers, to ligate the sperm duct as a method of alleviating prostatic hypertrophy. Favorable results had been reported in a great number of cases but Wallace remarks of these "When it is remembered how often cases of prostatic enlargement are greatly improved by rest and treatment of the accompanying cystitis, it is an open question whether the results above set forth were not to a considerable measure due to such treatment." From the literature on sex it would appear that the implications of such a statement are too infrequently considered in clinical work. Wallace performed vasectomy on the cat and dog and found that the testes in such cases were perfectly normal many months later than Bouin and Ancel would imply was a sufficient time to expect degeneration. Wallace concludes that single or double vasectomy has no effect upon the gametogenetic function of the testis; it continued to produce spermatozoa months and years after total occlusion of both vas deferentia.

Kuntz (80), on the dog, stated that thirty days after unilateral vasectomy the testis of the same side showed degeneration but also on the unoperated side as well. He conceived some influence operating through the nervous system that caused degeneration on the opposite side. Later experiments (81) on both the dog and rabbit were reported in which practically all animals showed testis degeneration as the result of vas ligation and resection. In control animals, however, Kuntz noted that the testes were likewise aspermatic and recognized that confinement and care of the animals was such that the unoperated tests were degenerate to about the same extent as those of experimental

animals. He then withdrew his former suggestion that sympathetic nervous influences set up by one degenerating testis caused the degeneration of the opposite one, but he allowed the idea to stand that within a month after operation the degenerate testis shows the influence from ligation of the vas deferens. Certainly no great weight can be attached to such conclusions when admittedly control animals do not show normal testes.

The greatest impetus to the conception of testis degeneration following vas deferens occlusion since Bouin and Ancel is the striking and apparently conclusive work of Steinach (1910-1920) culminating in his suggestive work on rejuvenation (183). Reviewed more in detail in a later section it may be mentioned here that the conception of the origin of sex hormones, from interstitial cells, and the properties of these hormones in producing youthful qualities in animals are the basis for his now celebrated rejuvenation hypothesis. By ligation of the vas deferens in rats Steinach reported degeneration of the germinal epithelium accompanied by an hypertrophy of the interstitial cells-- the hormone producing tissue; secondarily this stimulating hormone causes renewed germ cell production. Thus he believes that an animal so old as to have lost its germ cell production capacity is reinvigorated by a unilateral vas deferens ligation, and that the opposite testis following the stimulation begins to produce germ cells again and the animal returns to a functional condition. Steinach believes that ligation between the epididymis and the testis proper hastens the degeneration, and hypertrophy of the interstitial tissue. The fallacy here again depends upon operative manipulation of the organs in question, and an absolute disregard of the very many perfectly conclusive experiments showing the testis to be unaffected by

merely binding or severing the vas deferens. This will be further emphasized below.

Tiedje (190) follows Steinach in the belief of first a degeneration of the germinal epithelium then a regeneration after vasectomy. It should be pointed out, however, that neither Steinach nor Tiedje give substantial evidence to support their contentions. Wheelon (201), on dogs nine months after vas deferens occlusion, found that the testis contained all elements of the germinal epithelium. He believes either that all the tissue did not degenerate or that there might possibly have been a regeneration.

Sand (159) (161) (163) has studied the effects of vasectomy on the rat, guinea pig and dog, and has performed the operation in clinical practice, reporting eighteen cases of such operations on the human individual. In the latter, however, Sand follows Steinach's procedure and ligates between the epididymis and testis instead of merely occluding the duct. By this method he believes that the process of destruction of the germinal tissues is hastened. Sand (159) reported observations on vasectomy in rabbits, guinea pigs, and rats, summarized in tables in his paper; out of fifteen operated cases, some of which were observed for longer than a year, two cases only showed degeneration. Despite the fact that thirteen of his own operated cases failed to show degeneration, as against two that did give such evidence, he yet states a confirmation of the work of Bouin and Ancel that vas deferens ligation causes degeneration of the germinal epithelium and proceeds to employ the operation on man. Brack (27) however has shown that congenital absence of the vas deferens in man is without effect on spermatogenesis.

In this country Benjamin (12) has been perhaps the chief advocate of the Steinach

operation as applied to the human individual. In such cases histological studies are lacking but accepting the Steinach idea as proper and due to follow, Benjamin restricts himself to the clinical effects manifest in the patient. Clinical results will be granted by most individuals as being considerably conditioned by forced rest, good care, mental attitude, suggestion, and many other factors. And in view of the lack of proof of organic changes following this operation certainly one's credulity is stressed to the uttermost when it is maintained that the clinical results of this operation are alleviation of arthritis; lowering of blood pressure; reduction of prostrate (long ago definitely proven to be inefficacious); improvement of eyesight, and sclerosis of the inner ear; elimination of mental depression; improvement of sex impulse; and general restoration of spirits. We are led to believe that vasoligation first improves thyroid activity, and outside of this it influences "those glands that are most prominent or delinquent in the patients constitution."

The enormous literature on this subject (some only, being here given) is seen to abound in positive and negative assertions without any attempt to find the fundamental differences in technic or conditions that would in any way make the situation clear. Could we find an acceptable explanation to account for the cases of degeneration perhaps the entire findings would take on a different aspect and order be reestablished out of chaos. When, as did Cooper almost one hundred years ago, we find that a testis whose vas deferens was completely severed and occluded so that all materials produced by it are confined to the testis, epididymis, and the attached portion of the vas deferens and that the testis, is entirely normal except for distention of the epididymis with the seminal

products, then there appears to be no question whether ligation of the duct, of itself, produces degeneration of the germinal portion of the organ. Many things can be done to the testis that will cause it to lose its germinal epithelium in a very short time, for this organ is known to be a very labile one and to react to many unfavor-

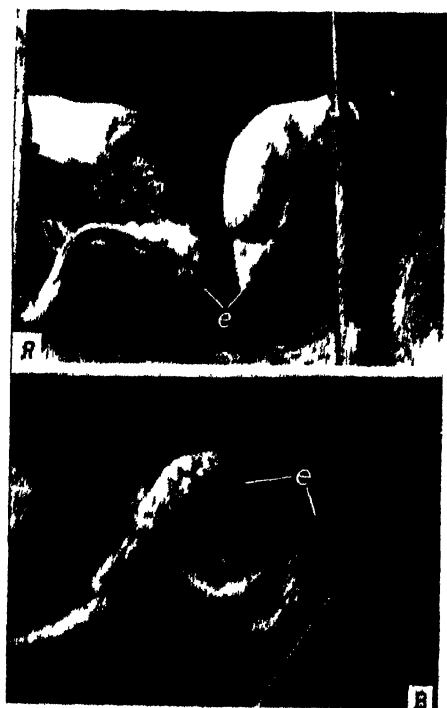


FIG. 6. PHOTOGRAPHS OF TWO ADULT RABBIT TESTIS.

A, testis on right, normal control; testis on left, vasoligation six months (note distended epididymis, e).

B, testis on right, abdominal retention six months; testis on left vasoligation six months (section of left testis in B shown in figure 1).

able conditions by loss of its germinal tissue.

In 1919 the writer sought to produce degeneration of the testes and compensatory hypertrophy of the interstitial tissue by vas deferens ligation in order to compare these testes with testis grafts. In the rat and guinea pig, however, degeneration

did not follow after operation (observations unpublished). The problem was further investigated by Oslund, then a graduate student in this department, and the first rational interpretation was given to results obtained following vasectomy (134). Correlation of results obtained with those obtained by the writer on the effects of displacement of the testis in experimental cryptorchidism (see section II) focused attention on the position of the testis following vas deferens ligation. Oslund was able to correlate all cases of degeneration following vas deferens ligation with an abnormal position of the testis where this was definitely known. Further experiments checking absolutely the position of the testis after operation showed that in every case the testis was normal if it resided in its normal scrotal position, but if it was held by adhesions in the inguinal canal or in the lower abdomen it was degenerate; a similar degenerate condition, however, followed as quickly if the vas deferens was intact but the testis abnormally situated. It follows therefore that degeneration was not due to occlusion of the vas deferens but to an abnormal position of the testis. Oslund later (135) confirmed earlier writers that vasectomy does not affect the dog testis if the dogs are not confined to close quarters, and that degenerate testes are often found in dogs confined but which have had no operation. Moore and Oslund (131) likewise confirmed earlier experiments on sheep vasectomy showing that the testes continued in active spermatogenesis months after complete occlusion of the sperm duct.

In order to test the hypothesis of an early degeneration of the epithelium followed by regeneration in vasectomy cases, Moore and Quick (129) performed the operation on a series of rabbits, studying the testes at intervals from thirteen days to

six months after operation. Spermatogenesis was normal after the operation and the retained products caused the epididymis to double or triple in size. Figure 6, *A*, shows the ligated testis of a rabbit in comparison with the normal one six months after vas deferens occlusion. One can readily see that the epididymis of the vas ligated testis is much larger than the normal. Figure 1, a section taken through the center of the testis shown in Figure 6, *B* (left), shows that the seminiferous tubules are normal and actively producing germ cells; testes removed thirteen days after operation were normal. There was no evidence that would lead one to assume an earlier degeneration of the germinal epithelium followed by a regeneration.

The enlargement of the epididymis tends to cause the testis to be elevated towards the neck of the inguinal canal and abdomen and on several occasions has been seen to result in the displacement of the testis into the abdomen. Because of the hypertrophied epididymis the testis sometimes does not immediately return to the scrotum and it should be remembered that artificial displacement of the testis into the abdomen for a very short period causes it to degenerate. In one case, we noted abdominal retention and consequent degeneration at six months. It must be emphasized, however, that this degeneration was not due to vasectomy but to abdominal retention. In other cases where purposely the testis was confined to the abdomen it was degenerate thirteen days after operation, but this is all that could be expected when the effects of abdominal retention are borne in mind. Thus it is again shown that ligation of the ductus deferens does not of itself cause the testis to degenerate, nor have we in this laboratory ever seen a case of hypertrophy of the interstitial cells following this

operation. Our studies involve more than a hundred vasoligations on rats and guinea pigs, twenty on rabbits, and four on sheep, with intervals of time from two weeks to longer than a year.

It should be emphasized that degeneration of the testis and the so called interstitial hypertrophy is the very basis upon which the idea of the efficacious measures of vas ligation are based and our experiments in this laboratory have been repeated on the same animals utilized by the originators of this hypothesis. With such facts in mind how are we to account for degeneration reported by other investigators? Emphasis should be placed upon the fact that the testis is an extremely labile organ and many apparent slight influences will cause its rapid degeneration. Mere confinement of the dog often leads to loss of germ cell production, which undoubtedly is temporary.

Our point of error has been adequately demonstrated by this laboratory, namely that of displacement of the testis from its normal scrotal position with consequent degeneration from experimental cryptorchidism and not from vas deferens ligation. This is very prone to happen in animals whose testes have an open pathway from the scrotum to the abdomen, as the rat, rabbit, and guinea pig; and the majority of degenerations reported have come from this series of animals. Manipulation of the testis where trauma is involved often causes the testis to be retained partially or wholly in the abdomen. The effect of this has been known since Griffith's time but it is easily forgotten and neglected. It was so in this laboratory, and only the first hand dealing with such operations coincident with vasectomy served to impress the fact sufficiently that slight displacements were to be taken seriously. No doubt a great number of degenerations following vasectomy

are due to this factor. Operation on such animals should be done through the abdomen where the vas can be ligated close to the testis without touching the testis or with drawing it from the scrotum; operation though the scrotum itself should be rigorously avoided if uncomplicated conditions are desired. Even with a clean operation on the vas deferens, where by all means the artery of the vas deferens is to be avoided, adhesions have occurred that caused testis elevation. This condition leading to degeneration must be clearly separated from the effects of the occlusion of the vas deferens. All blood vessels running to and from the testis should be avoided. Many workers have given no heed to this complicating factor and have ligated the entire spermatic cord. It should be no surprise that degeneration follows such a procedure in the testis for organs deprived of their blood supply will undergo degeneration whether they be liver, kidney, brain or spleen.

Steinach and Sand severed the testis from the epididymis believing that by this method degeneration occurred more surely and more rapidly. Van Wageningen (193) recently studied this method of blocking the testis outlet and notes degeneration of the testis in 106 cases in the rat. In a later paper (194) however she states that her operations were followed by hardening of the testis from congestion, and that the lack of oxygen and food was undoubtedly sufficient to cause such destruction as was obtained.

The lack of proper controls has in some cases led to misrepresentations of the effect of occluding the outlet duct. And finally many apparently trivial conditions can become complicating factors and give results that are wrong in implications unless particular attention is given to the fact that the testis is affected adversely. Insufficient attention to apparently minor

details is the structure upon which has been builded the erroneous hypothesis that occlusion of the duct of the testis leads to the degeneration of its germinal epithelium. Belfield (10) has recently restated the conditions obtaining in man where the vas deferens has been totally occluded. Thus "In a large majority of subjects sperms have been found there (epididymis) even from five to seventeen years after the occluding epididymitis occurred; in these cases, therefore, atrophy of the spermatic tubules had not occurred" (page 12, 12).

Founded on error, therefore, and abundantly disproved on every species of mammal where degeneration after vas ligation has been reported, it would seem that the operation as applied to man for purposes of rejuvenation should have well run its course—at least so until adequate proof of some biological principle is involved to justify its utilization. At present it may be emphatically stated there is no biological justification for the operation that has been established by experiment. The testis neither undergoes rapid degeneration solely on account of blocking the outlet from it, nor does this operation affect in any detectable manner the condition of the interstitial cells. It is now well understood that many influences can cause degeneration of the testicle, and that in the majority of such cases of degeneration the interstitial cells appear to be more abundant. In infarction of the liver or kidney, areas of degeneration of parenchyma can be seen accompanied by a proliferation of connective tissue, but as yet this method of clinical procedure has not been employed as an efficacious measure. Granting there may appear to be an interstitial cell increase, it is yet to be proven that such has any influence upon the organism. Until such a condition is proven there is no justification in accepting in principle an efficacious result

from any method that causes the testicle to degenerate. This is dealt with more in detail in a following section.

IV. TESTIS TRANSPLANTATION

Transplantation of the mammalian testis has been studied for many years and the development of our present knowledge of the best technic, of the possibilities of the reaction of the transplanted tissue, and of the efficacy of the procedure has been a fascinating topic.

The earliest attempt to transfer the testis from one organism to another with notable results dates back to 1849. In that year Berthold (17) published his notable contribution on the autoplasmic and homoplasmic transplantation of the bird testis. Testes placed within the coils of the intestine and removed six months later contained spermatozoa capable of movement. About forty years later Berthold's observations were confirmed for the same animal by Loge (96), Hanau (64), and Foges (48). It was found that the bird testis graft persisted in a functional condition not only in the abdomen, its normal location, but also in subcutaneous areas wherever it could obtain a vascular supply: underneath the skin the spermatogenetic function continued and motile spermatozoa were produced.

Following this earlier successful bird work, both amphibian and mammalian transplantations were studied, but in the latter, expected successes did not easily follow. Many workers were able to successfully transplant mammalian ovaries and it was realized early that these could be transplanted with much greater ease than could the testis. Ribbert (155) was unable to transplant the testis of the rabbit or dog and obtain persistence of the graft. Within a very few days after transplantation he noted that the seminiferous tubules underwent degeneration and

rapidly lost their germinal epithelium; in some cases the epididymis tubules could be found in a relatively normal condition but more often all the graft was resorbed and replaced by connective tissue. Ribbert believed that it was impossible to transplant the organ successfully because of the fact that its functional products were discharged to the outside. Gobell (53) likewise failed to obtain persistence of transplanted testes of the rabbit and guinea pig. The grafts rapidly became necrotic and gave no evidence of a capacity to persist and carry on their spermatozoon producing function; the contents of the seminiferous tubules at the time of transplantation were rapidly absorbed. Foa (47) failed in his attempt to transplant the dog testis and he was firmly convinced that the testis could not be transplanted and persist. Cevolotto (35) was somewhat more successful with the rabbit; grafts recovered forty-five days after subcutaneous transplantation consisted of a few degenerate tubules. Practically all the germinal epithelium was destroyed by a process of sloughing into the lumina of the tubules and subsequent degeneration. Castle and Phillips (33) had negative results in thirty-three attempts to transplant young rat testes into the empty scrotum of an older castrated rat.

Beginning with the work of Steinach better results were obtained in transplantation of the testes (177 to 183). In 1910 he reported the successful persistence of autoplasmic testicular grafts but in all cases the seminiferous tubules were entirely abnormal in as much as only tubule outlines containing a few Sertoli cells were present instead of the normal germinal content characteristic of the organ. He states that in all testis grafts the germinal portion is lacking and that the most prominent tissue is the interstitial tissue composed largely of the cells of Leydig;

these he considers to be the source of the sex hormones (see later section).

Voronoff (196) has transplanted the testes of goats, rams, and man. Retterer (151) (152) describing these grafts recovered by Voronoff from the goat and ram mentions that the majority of the grafts are degenerate; may times there is only connective tissue, but in others well defined tubule outlines are present with at times traces of the germinal epithelium. One testis graft from each, the goat and the ram, are said to show a fairly normal epithelium within the seminiferous tubules and to contain bodies believed to be sperm heads. This was true in the goat graft (removed from the scrotum) after a period of persistence of about two weeks. It may be questioned, however, whether this graft represents possible retention of completely differentiated products at the time of transplanatation; it is conceivable, in the absence of other grafts to substantiate the idea, that this graft represents a retention of previously formed products rather than the differentiation of new products after transplantation. This short period of time leaves the implication of the findings somewhat in question. A longer persisting ram testis graft showing fairly normal seminiferous tubules containing sperm head-like bodies, is also open to question for the reason that the graft was fastened to the normal testis of the host. In removal of this graft it may be questioned whether a portion of the normal testis in situ was adherent to what was supposedly the original transplanted tissue.

The short account of Retterer was unknown to Moore (119) when he stated that for the first time mammalian testis grafts were obtained which had differentiated spermatozoa. If the implications of Retterer's account are correct then this was actually shown two years

earlier. It makes little difference whether actually correct or not, the significant thing, and the point contended for by Moore, is that there exists but one locality in the mammalian body where grafts have proven capable of producing spermatozoa. This locality is the scrotum, and its significance is discussed in section V.

Sand (157, 158, 162, 164) has reported his experiences many times with transplantation of the mammalian testis, using chiefly rats and guinea pigs. His general results on histological persistence of the testis grafts differs in no material way from those described by Steinach, except that he does mention (164) that sometimes the germinal epithelium may be partially preserved and contain spermatogonia and spermatocytes.

The results of testis transplantations in this laboratory were at first similar to those described above (Moore 115, 116); grafts consisted of degenerate seminiferous tubules containing only Sertoli cells, and many times an apparent overdevelopment of interstitial cells though it was recognized that the latter did not always follow. Figures 7 and 8 are reproductions of small portions of two grafts obtained from transplantation of the testes into spayed female guinea pig. It is evident from figure 7 that seminiferous tubules lack a germinal epithelium except for the single basal row of Sertoli cells; interstitial cells appear to be developed in an overabundance. Figure 8, however, is an exceptional type and shows that active spermatogenesis has continued despite the fact that the graft resided in the spayed female for a period of nine months. The interstitial cells in comparison with figure 7 are minimal in amount and approach the condition of this tissue in the normal testis. From this the question arose why spermatozoa were never found in transplanted mammalian testes; Berthold had obtained

bird testis grafts with spermatozoa. If found? It can be seen (*a*, fig. 8) that the in mammals the earlier phases of spermatogenesis were never found. The lumen of some of the tubules contained

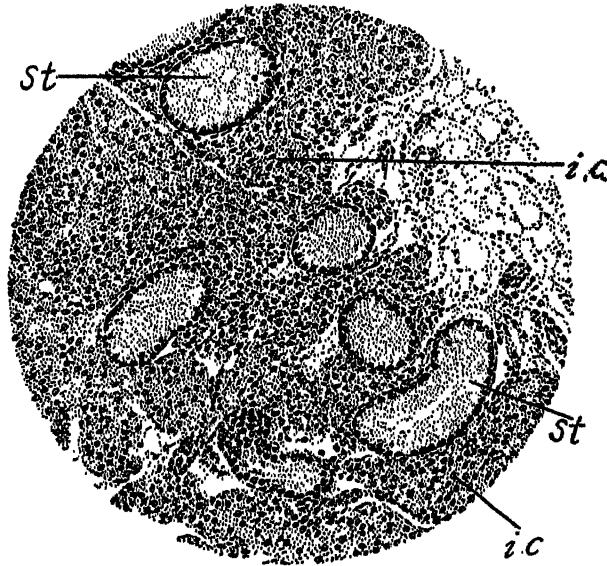


FIG. 7. GUINEA-PIG TESTIS GRAFT (PERITONEAL) SEVEN MONTHS IN SPAYED FEMALE
st, interstitial cells; *st*, seminiferous tubules

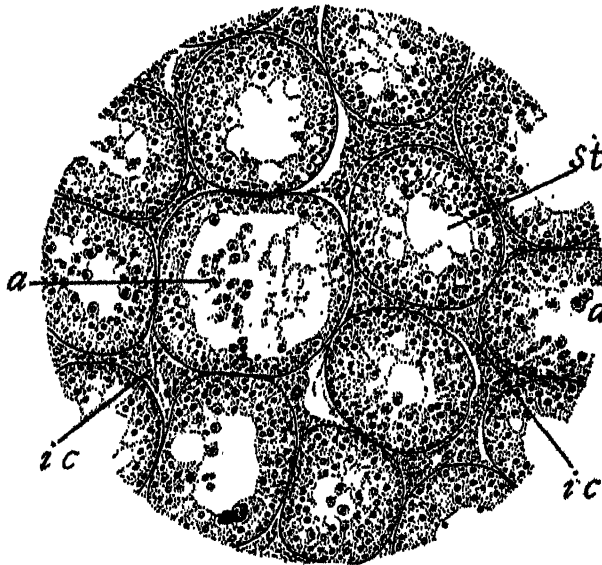


FIG. 8. GUINEA-PIG TESTIS GRAFT (SUBCUTANEOUS) NINE MONTHS IN SPAYED FEMALE
a, cells sloughed from epithelium into tubular lumen; *st*, interstitial cells; *st*, seminiferous tubules.

genesis continued actively, why were later loosened cells in stages of degeneration. stages with actual spermatozoa never On closer observation it could be seen that

these were gradually escaping from the medial edge of the epithelium into the lumen where they underwent fragmentation and solution; they appeared to have lost their capacity to adhere to the epithelial strata and build this to completion. The answer to this puzzling question did not receive its explanation until the first results were obtained on experimental displacement of the testis into the abdomen (see section II).

When it was forced upon the attention that a normal testis in a stage of active spermatogenesis will undergo rapid degeneration within six days and lose all its germinal epithelium within a period of twenty days if it is placed in the abdomen, it was only logical to account for the lack of the the germinal portion of the testis grafts as being due to their abnormal environment. An apparent discrepancy should be made clear. It has been found that a testis displaced from the scrotum into a subcutaneous environment is entirely different structurally from the opposite one displaced into the abdomen. And whereas many grafts previously described in the literature have been made intramuscularly and intraperitoneally the one shown in figure 8 was a subcutaneous graft.

Following this condition further, and testing the hypothesis that the scrotum has a very definite and decided influence upon the process of spermatogenesis, the writer has carried out an extensive series of testis transplantations in different localities in the body (125). More than one hundred rat testis grafts from intraperitoneal, subcutaneous, intramuscular and scrotal positions were recovered; spermatogenesis continued in many grafts up to the spermatocyte stage and mitoses proved that active division of the germ cells continued. The newly formed cells however did not adhere and produce a

complete epithelium but instead they escaped from the epithelium into the lumen to degenerate. Testis grafts, in the scrotum, were many times similar to grafts from other localities but several of the scrotal grafts showed normal seminiferous tubules. These tubules contained a normal, active germinal epithelium, many cells of which were in stages of mitosis and spermatozoa were present in quantities similar to normal testes. In these cases there is no question that differentiation continued in the graft. The testes transplanted were taken from animals two to ten days after birth, at which time the tubules are embryonic in development, and they were transplanted onto the tunica vaginalis of totally castrated males; in sections of the grafts the remains of the old ligature can be seen. These grafts were removed two to six and one-half months after transplantation.

These facts teach us therefore that a mammalian testis graft can develop spermatozoa provided it is transferred to a locality where such is possible. To date the scrotum is the only locality where such differentiation has been obtained, and since it fits in so consistently with the many other elements of proof for the function of the scrotum, we have good reason for suspecting that it will prove to be the only locality in which germ cell differentiation can go to completion.

One of the many debatable points arising in sex gland transplantation has had to do with the possibility of successfully transplanting a gonad into an animal of the opposite sex. Herlitzka (70) and Schultz (165) were to my knowledge the first workers to attempt, with successful results, such transplantation in the mammal. Each, working with the guinea pig, succeeded in transferring the ovary into normal males and recovered later the

ovarian graft. Herlitzka in particular mentions that the ovarian graft is not hindered in its incorporation or persistence by the normal testis of the male host. Basso (9) likewise recovered ovarian grafts from normal male rabbits; they persisted as satisfactorily as when transplanted into females and contained normal Graafian follicles in all stages of development. Marshall and Jolly (106) were able to transplant the ovary into a male rat with limited success. Cevalotto's (35) grafts of the testis into subcutaneous positions in the female rabbit persisted as well as when graft d into males.

Steinach was unable to obtain persistence of a gonad of the rat or guinea pig after its transfer to a normal animal of the opposite sex. Thus he could successfully transfer an ovary into a male animal previously castrated, or a testis into a previously spayed female, but he could not obtain persistence without previous elimination of the normal glands of the host. In 1916 however he was successful in transplanting simultaneously an ovary and a testis into a previously castrated animal.

Around this series of results Steinach constructed his hypothesis of antagonism between secretions from the two opposite sex glands. He believed each gland produced a substance that acted adversely on the opposite sexed organ, and that this influence was sufficiently potent to prevent, for example, the growth of an ovary in a normal male or the growth of a transplanted testis in a normal female. When the environment was neutral, however, as might be conceived to follow elimination of the normal gonad from either animal, then simultaneous transplantation of the two opposite sexed organs into the neutral host would be followed by incorporation and growth of each. Thus he believed that the antago-

nistic forces were somewhat overcome, that each had an equal chance of incorporation and persistence.

Sand like Steinach was unable to obtain incorporation of the gonad of one sex in a subcutaneous position in a normal animal of the opposite sex; with removal of the normal gonads of the host such could be obtained. However, by transplanting an ovary into the substance of the testis he found that the ovary graft persisted and carried on its differentiation in a normal manner, and the testis likewise remained normal and produced spermatozoa. He thus saw an inconsistency in Steinach's antagonism hypothesis, but there was still to account for, his failures to obtain growth of the graft in other parts of the body without first removing the host gonad. To account for this Sand developed his hypothesis of "atreptical immunity."

In brief, Sand conceives that the body elaborates a specific food substance essential for growth of the sex glands, but a non-sex specific substance that either gland could utilize. This substance, he believes, is rapidly removed from the blood stream and stored within the organ in question. Therefore, he believes that a normal testis would so completely remove the specific substance, storing it within the gonad, as to make it unavailable for the ovary transplanted into a subcutaneous position and this graft perishes because of starvation for it. If however the ovary is placed within the testicular substance this specific food substance would be available to it and persistence follows.

It will be realized, therefore, that both Steinach's "antagonism" hypothesis and Sand's "atreptical immunity" hypothesis were constructed primarily to account for their failure to obtain growth and persistence of gonads transferred to normal animals of the opposite sex. In this

laboratory, however, we have not found the need for such hypotheses. Moore (115) reported successful results from transfer of ovaries into male rats that retained one normal testis, and testes transplanted into females with one ovary present. It was our earlier custom to operate simultaneously on a young male and female of the same age, removing one testis from the male to the female, and one ovary from the female to the male; thus each animal retained one of its normal sex glands and the transplanted gland of the opposite sexed animal. Many months after the operation such ovarian grafts from males with one testis present were found to be carrying on their normal differentiation, from the fact that normal Graafian follicles of all stages of development were present, even to stages showing maturation of the ovocytes; the single intact testis of the male was entirely normal and the animal was utilized as a breeding male. Similarly the testis grafts were recovered months after transplantation from the female whose single ovary remained in place and functional. These testis grafts, for the reason that they were in intramuscular and intraperitoneal positions were not in a normal condition but were entirely similar to grafts from such localities in castrated males. Moore called attention to the superfluousness of hypotheses explaining lack of such persistence in as much as no difficulty was experienced in obtaining persistence of the graft in the opposite sexed animal.

Bohn (21) reviewing Moore's results and contentions saw in the experimental procedure a confirmation of Sand's hypothesis. In as much as he takes for granted the necessity of removal of one sex gland before the gonad of the opposite sexed animal would survive Bohn argues that removal of the one gland would allow sufficient amounts of the specific food sub-

stance to be left in the general circulation and the opposite sexed transplant could therefore persist. Moore (120) however pointed out the fallacy of this reasoning by citing preliminary results of later experiments wherein such transplantations were carried out successfully without interfering in any way with the normal intact gonads of the opposite sexed host (see 125). Thus in a large series of testis grafts many of which were transplanted into normal females, such grafts persisted for months and when removed were found to contain seminiferous tubules in active spermatogenesis: the cells produced by mitosis in the germinal epithelium escaped into the lumina of the tubules and degenerated, in all essentials the exact counterpart of tubular activity in grafts located in castrated males. This condition holds, moreover, even during the course of pregnancy. Testis grafts have been removed from at least ten normal females that had completed the period of pregnancy, delivered and suckled normal litters of young and were killed immediately on weaning; the grafts in such cases have persisted for months after transplantation. The same has been found in many other normal females that had not been bred.

Thus it is seen that neither the two ovaries nor even the condition of pregnancy itself has any apparent deleterious influence upon spermatogenesis so far as this function can be consummated in the environment in which the graft finds itself. Grafts made in similar positions in the normal male, normal female, pregnant female, or castrated male appear to have the same capabilities of growth and persistence as well as of differentiation; it is to be remembered, however, that the graft placed in the scrotum can complete differentiation and produce normal tubules containing spermatozoa.

V. THE FUNCTIONAL SIGNIFICANCE OF THE SCROTUM

Preceding sections have directed the attention to some conditions under which a testis fails to continue its normal gametogenetic function. Thus undescended testes of scrotal animals do not produce germ cells and double cryptorchidism is accompanied by sterility; removal of healthy functional testes from the scrotum to the abdomen results in rapid and complete destruction of the germinal tissues, and return of a testis in a degenerate condition from the abdomen back into the scrotum permits of recovery and return to a normal functional condition, whereas a testis intermediate between the two cavities may likewise show an intermediate condition from degenerate to normal; ligation of the vas deferens does not affect the normal function of germ cell differentiation provided the testis suffers no displacement from its normal position by adhesions or other factors unrelated to mere occlusion of the excurrent duct; and finally testis grafts are found capable of producing spermatozoa only when transplanted into the scrotum. In each case, therefore, the common factor is an association of the testicular tissue with the normal scrotal position for the organ. With this information derived from experiments before us, the work in this laboratory was directed to the study of the nature of the causes for germ cell degeneration when the organs are extra-scrotal in position. Why do undescended testes fail to develop normally? Why do testes removed from the scrotum to the abdomen undergo rapid and complete germ cell degeneration? Why do testis grafts complete their normal development only when placed in the scrotum?

By experiment all hypothetical factors were eliminated as primary causes of germ

cell degeneration except the possibility of higher abdominal temperatures, or conversely lower scrotal temperatures. While experiments were in progress to prove or disprove the differential temperature hypothesis Crew (41) on hypothetical grounds advanced the suggestion that the aspermatic condition of improperly descended testes might be due to higher temperatures in the abdomen than in the scrotum.

Several means suggested themselves to prove or disprove the idea, among which were investigations (1) to ascertain if real differences in temperature did actually exist in the two localities; (2) to determine if prevention of heat loss from the scrotum affected the welfare of the organ; and (3) to study the effect of applying temperatures somewhat higher than normal to the scrotum or testes direct.

a. Scrotal and abdominal temperatures

It is well known from the experiments of Benedict and Slack (11) that a temperature gradient exists in man, from the deeper cavities of rectum and vagina to the external skin, of approximately 5°C. It has also been stated that temperatures within the scrotum were less than in the abdomen without citations of such observations. Moore and Quick (128) however, determined that the interior of the rabbit, rat and guinea pig scrotum was invariably some degrees cooler than the interior of the abdomen. This difference, detectable at ordinary laboratory room temperature, increased as the external environmental temperature diminished. The guinea pig and rabbit scrotal temperature was 1½° to 3°C. lower than abdominal temperatures at a room temperature of 30°C. but this difference was more marked in the rat. Thus in the white rat observed in a room temperature of 16°C. it was found that the interior of the scrotum

was 7°C. lower than the interior of the abdomen.

Thus direct proof is afforded that the actual normal environmental (scrotal) temperature is lower than that of the general body temperature and the hypothesis is greatly strengthened that a differential body temperature is the causal agent in testicular degeneration when the organ is abnormally situated in reference to the scrotum.

b. Scrotal insulation

The fact of a differential temperature in the abdomen and scrotum necessitates the assumption that the scrotum is a local thermoregulator serving to control the temperature around the testes. If such a regulatory mechanism is essential for normal testicular activity it should follow that prevention of the control would be fatal to the active elements of the organ. Moore and Oslund (131) choosing the ram with its large pendent, pear-shaped scrotum as the most suitable animal for experiment, carefully covered the scrotum first with a layer of woolen batting, second with a layer of heavy woolen cloth, and finally with a layer of waterproofed canvas material. Sewing each layer separately so as to closely fit the external scrotal contour it was believed that at least a part of its regulatory function might be done away with. Care was exercised to prevent encasing materials from sagging upon, or binding, the scrotum; supports over the animal's back allowed the scrotum to hang its full length and at all times a finger could be passed inside the covering. The animal was sacrificed ninety days after the scrotal wrappings were applied, meanwhile running freely in a barnyard. Sections from different regions of the testis showed that the scrotal insulation produced a decided degeneration of these

organs. No normal seminiferous tubules were found in the testis nor could spermatozoa be seen from any region of the testis proper. The cells of the germinal epithelium had either been entirely removed or could be seen in stages of degeneration. The lumina of many tubules contained degenerating masses of cells thrown out from the epithelium.

We thus see that prevention of the thermoregulatory function of the scrotum causes an animal to sterilize itself with its own body heat. The germinal tissue destruction is highly similar to that found in experimental cryptorchidism. This result alone would appear sufficient to definitely establish the function of the scrotum as a local thermoregulator, and a scrotal position as indispensable to the normal activities of the testes in those mammals normally developing a scrotum.

c. Heat application

As confirmative proof of the effects of higher temperatures upon the welfare of the testis, artificial sources of heat have been applied externally to the scrotum as well as directly to the testis itself. Moore and Chase (126) reported that external application of higher than normal body temperatures to the scrotum was followed by degeneration of the testes. Discussing the effects more in detail Moore (123) showed that single exposures to water approximately 7°C. above normal body temperature, running over the scrotum, was followed within five to ten days by extreme degeneration of the testes. Graded effects of this influence were obtained by varying either the length of application of heat (using warmed water, electric stove, or electric light) or the degree. Testes suspended in a normal saline solution 6° to 7°C. above normal body temperature for five minutes suffer the loss of practically all the ger-

minal cells within ten days. Similar exposures of testes to saline of a few degrees below normal body temperatures leaves the testis normal. It is the higher temperature, therefore, and not the operative procedure that is the cause of degeneration.

The Japanese worker Fukui (50, 51, 52) determined that testes of the goat, rabbit, guinea pig and rat degenerate rapidly after exposures to artificial heat slightly above the normal body temperature. Fukui employed as sources of heat an electric arc, sun light, hot water, hot air and paraffine. Particular emphasis should be given his findings that a testis elevated to the abdomen requires approximately the same length of time for degeneration as does a testis to which the equivalent of body temperature is applied externally to the scrotum. A second point of particular importance is his findings on artificially cooled cryptorchid testes. In the dog he found that when both testes were replaced in the abdomen and an artificial cooler applied to the ventral abdominal wall in the region of one testis, the testis in the artificially cooled region remained normal while the uncooled one degenerated.

With the accumulated data from so many and varied types of experiment bearing directly on the condition of the testicle we may now regard as proven that temperatures within the abdomen are above the optimum for spermatogenesis. Thus we have an explanation of conditions inherent in undescended testes; we have a partial solution for the behavior of testis grafts; and we see an explanation for perhaps most of the incorrect conclusions on the effects of vasectomy.

d. The significance of the scrotum

Appearing only in mammals, the hitherto unexplained conditions of scrotal forma-

tion, and testicular descent, appear in a new light. Thoroughly appreciating the fact that the lowest mammals (monotremata) retain the reptilian and lower vertebrate type of abdominal testes, a survey of mammalian forms forces attention to a gradual evolution of the scrotum and testicular descent. The marsupials, more or less specialized in many ways, are likewise aberrant in scrotal formation in as much as the scrotum is perpenial and of a somewhat different type than that found in other mammals. Many edentates, like the monotremes, retain the testes in the abdomen normally, as do some of the insectivores. Certain members of different lower groups of mammals have a seasonal spermatogenetic cycle at which time the testes are either in contact with a thin area on the abdominal wall or lie in a relatively temporary scrotum. The active production of germ cells is therefore correlated with this simple scrotal beginning (Rasmussen, Tandler and Gross, Marshall, Griffiths, Hansemann, etc.). Recession of the organ from this temporary scrotal position is followed in general by loss of capacity to produce germ cells. Among rodents (rat, rabbit, guinea pig, etc.) the testes usually have passed through an inguinal canal into a scrotum but separation of the latter cavity from the abdomen is not complete; the inguinal canals remain patent throughout life and the testes can be elevated into the abdomen and redescend into the scrotum. Terrestrial carnivora possess the closed scrotum but in some aquatic carnivora the testes remain in the abdomen. The majority of the ungulata show a typical descent into the scrotum but again several members of this group retain the testes in the abdomen (hyrax, elephant, rhinoceros). Abdominal testes also exist in some of the more highly specialized aquatic forms (cetaceans and sirenians) but primates

normally carry the scrotal development to completion and the closed inguinal canals prevent reentry of the descended testis into the abdomen.

There is thus revealed in general a correlation of scrotal development and mammalian evolution but as in the evolution of so many structures (appendages, teeth, etc.) Variations have occurred. Such an evolution is not necessarily invariably associated with the acquisition of higher body temperatures for the bird, with its slightly higher temperature than mammals, has retained the testes in the abdomen.

Without attempting to explain the cause of such an evolution in terms of one hypothesis or another attention may be directed to the structural characteristics of the scrotum that would fit it for such a thermoregulatory capacity. Primarily an outpouching of the peritoneum against a thin area of the abdominal wall, continued elaboration has produced a sac like structure lined by the tunica vaginalis, a derivative of peritoneum, covered by an extremely thin integument well provided with sweat glands and without subcutaneous fat. Active adjustment to external temperatures can be noted in many animals by the great relaxation of the scrotum in hot weather as against its decided contraction in the cold; within certain limits the amount of relaxation and consequent separation from the body is a function of the external temperature. That it does function to reduce the environmental temperature of the testis has been proven by Moore and Quick, and it is now fully appreciated that such an adjustment is essential for those mammals normally developing such a structure.

Data for a consideration of the possible relationship between degrees of scrotal formation and the body temperature of the animal are not available, but it would

appear probable that in many animals lacking the scrotum the body temperature would be of a variable character and subject to wider fluctuations than would occur in those forms where complete descent into a well formed scrotum has taken place. Different degrees of degeneration by abdominal replacement of the testis of rats and guinea pigs correlates with a less restricted range of body temperature. Temperatures against the internal body wall of the rat were found to be a degree or more lower than among the viscera in a deeper position; the variations in this respect are greater than are those found in the guinea pig. Correlated with this fact we find that abdominal testes of guinea pigs are injured considerably more in a given length of time than is the rat testis; guinea pig testes elevated into the abdomen for a period of two weeks are usually more degenerate than the rat testis similarly treated for six months. But yet in the guinea pig, despite the total loss of the generative portion of an abdominal testis in two weeks, a testis graft subcutaneous in position may continue its early stages of spermatogenesis and build an epithelium practically normal in its cellular content for a period of nine months (see fig. 8).

We are justified in concluding, therefore, that in the evolution of mammals a condition has been produced such that the testes cannot carry on their primary function when exposed to the normal abdominal temperature. There has been a gradual recession of the organ posteriorly where first it comes to lie against the anterior abdominal wall in a cooler and primitive scrotal-like area. Carried farther this primitive beginning has gradually become more pronounced and in the higher forms the scrotum with its special structural peculiarities becomes closed off from the abdomen and provides within its interior

a temperature environment lower than that in the abdomen. Along with this newly acquired structure and function the testes of higher mammals depend upon the very conditions that are provided. Without this thermoregulatory function the testes cannot produce spermatozoa. Removed from the cooler environment of the scrotum, or so interfering with the scrotum that it cannot regulate the temperature about the testes, the organ cannot perform its primary function in the general economy of the animal body—that of producing spermatozoa.

VI. THE EFFECTS OF ROENTGEN RAYS ON THE TESTIS

The discovery of the X-rays by Roentgen in 1895 and the accidental effects upon the skin in producing inflammations and dermatitis caused attention to be focused on these, particularly their effects upon the organism or individual parts of it.

The destructive effects of the X-rays on the gonads, more or less accidentally, discovered by Albers-Schonberg (1) has led to considerable experimental work on the reproductive glands. Albers-Schonberg exposed male rabbits and guinea pigs to X-rays and failed to obtain offspring in subsequent matings with untreated females; sterility was due to a lack of spermatozoa in the testes. A few months later Friebe (49) reported that the seminiferous tubules were reduced in size, and that the lumina of the tubules often contained loose cells in a state of degeneration; there was an entire lack of mitoses in the cells of the tubules.

Brown and Osgood (30) reported that the mere presence of men in an X-ray room, either as operators or helpers, led to an azoospermic condition. Phillip (138) similarly reports that X-rays cause sterility in men. One, a tuberculous individual, voluntarily submitted to daily ex-

posures of from ten to fifteen minutes for thirty days. Whereas motile spermatozoa were obtained for a considerable time after the beginning of the exposures it was found at the end that the testes were entirely devoid of spermatozoa (hyperdermic syringe sample); under the limits of the observation the individual reported no diminution in sexual capacity, despite his sterility. In 1904 and 1905 Bergoigne and Tribondeau noted that X-rayed testes of the white rat were rendered superficially translucent, and that fluids issued from any cut surface of the organ. Later this edematous condition disappeared and the seminiferous tubules were found to lack a germinal epithelium, or at most contained only a few spermatogonia. The degree of destruction in the testis was roughly proportional to the X-ray dosage.

These writers noted a high degree of selectivity of the X-rays for the germinal portion of the gonad and that Sertoli cells appeared unaffected; the latter were not only present after all germ cells had been eliminated but were increased in number through amitotic divisions. They state that Sertoli cells may thus multiply and increase in number but are incapable of producing cells of the germinal line. Three months after the last exposure to X-rays they were unable to find any germinal cells in the testis; the interstitial cells were overabundant. They believe the X-rays act upon the individual cells directly; that rapidly dividing cells are more easily affected; and that spermatozoa are unchanged by such exposures. Indeed they determined that human spermatozoa exposed directly to the rays for thirty minutes suffered neither change in form nor loss of motility. A single exposure of the rat testis was sufficient to render the animal sterile.

Villemin (1925) confirmed the main

contributions of Bergoigne and Tribondeau. Guinea pig testes exposed to X-rays suffered complete destruction of the seminal tissue but interstitial cells were unaffected; such animals retained their sexual ardor. Villemin determined that a smaller dosage was followed within three and one-half months by regeneration of the testis and production of spermatozoa. He maintained that as long as spermatogonial cells remained in the degenerate testes recovery of normal function was possible, but without spermatogonia no recovery could take place; Sertoli cells were incapable of producing the cells of the seminal line.

In a series of papers Regaud and Blanc (145), Regaud and Dubreuil, (146, 147) Regaud and Nogier (148), the earlier studies on X-ray effects on the testis were confirmed and extended. Exposures of young rabbit testes before differentiation did not subsequently alter testicular development, whereas in the differentiated testis complete sterility was produced; but despite sterility there was no diminution in sexual ardor. Those receiving X-ray exposures copulate and at first discharge motile spermatozoa, but these appear incapable of fertilizing ova; later, spermatozoa were absent from the semen.

Subsequent X-ray work on the testicle by Harvey (67) Herxheimer and Hofmann (71) Wakelin Barratt and Arnold (199), Hewer (72), and Ancel and Bouin (4) give added confirmation of the selective, destructive action on the germinal portion of the testes. Simmonds (171) determined that mesothorium acts similar to X-rays. Wakelin Barratt and Arnold describe intimate changes in the individual cells following exposure. All workers are in agreement that selectivity is the outstanding event. Cells of the seminal line show no changes for the first twenty-four hours after exposure; subsequently the

protoplasm becomes somewhat cloudy and approaches a general aspect of coagulation; nuclei, especially those in mitosis, show many abnormalities. In general two different types of disposition of the germinal tissue is observed. First there is a local cytolysis of cells *in situ* leading to a liquefaction of material and the consequent vacuolated appearance of the epithelium. The products of cell cytolysis are absorbed into the blood stream. Accompanying this condition there is a second one in which many or most of the remaining cells are sloughed into the lumen of the tubule. Such masses of material contain cells little modified, cells showing degeneration changes, and a considerable mass of debris from cells that have undergone partial solution or fragmentation. Some of the cells thrown out into the lumen may be carried into the epididymis where their further degeneration and absorption can be followed.

The type of behavior in the X-rayed, degenerate testes is highly similar to the type of degeneration encountered in testes confined in the abdomen. Cell changes, the local cytolysis, sloughing into tubules, transportation into the epididymis, the retention of spermatozoa in the vas deferens are all common conditions in degeneration from the two different causal agents. The selective action on the seminal line and the retention of Sertoli cells and interstitial elements are common to the two types. Shrinkage of the seminiferous tubules and the apparent interstitial hypertrophy are entirely similar. Finally the powers of recuperation of the testes from spermatogonial elements gives a series of conditions that would make it almost impossible in a study of degeneration to decide between the two causal agents. These similarities force themselves on our attention as well

as the fact that the real causal effect in each case is not apparent. We know neither the ultimate cause of degeneration as produced through testis elevation to the abdomen or the external application of higher than normal temperatures, nor the actual ways in which X-rays produce their effects. It may ultimately be proven that the similarities are more than superficial and that the two causal agents may have a fundamentally similar action upon the protoplasm of this labile tissue.

VII. HYPERSENSITIVE REACTIONS IN THE TESTICLE

An interesting testicular reaction but recently discovered, and bearing so great a similarity to reactions heretofore considered, is that used by E. R. Long and his student. Long (97) determined that guinea pigs experimentally infected with tuberculosis of mild virulence intraperitoneally or in the axilla, twenty days or longer, show a most striking reaction when one testis is reinoculated with tubercle bacilli. Within twenty-four hours the inoculated testicle becomes swollen and extremely hyperemic and edematous. Sectioned, the testicle shows marks of degeneration of the germinal tissue and within one month practically all germinal cells are destroyed. The opposite uninjected testicle, or an injected testicle in a nontuberculous animal, does not exhibit the inflammatory reaction or degeneration. Carrying the observations farther Long showed that intra-testicular injections of tuberculin (0.01 cc. O.T.) into previously mildly infected animals was similarly followed within twenty-four hours by great swelling, edema, hyperemia, and early sloughing of the germinal portion of the seminiferous tubules; within four weeks after such injections all germinal cells with the possible exception of spermatogonia have been removed from

the organ. Along with the tubular degeneration "... the interstitial cells (of Leydig) have proliferated in a striking manner." "At this period (24 hrs.), when the testicle of the previously infected guinea pig is so highly inflamed, the testicle of the noninfected one shows little or no change either grossly or microscopically. Tuberculin, so destructive to the testicle of the infected guinea pig, is absolutely nontoxic for the testicle of the normal animal." Spermatocytes and spermatids appeared the more susceptible, spermatogonia and spermatozoa more resistant. Similar reactions to other hypersensitizing agents are reported by Long and Seyfarth (98) and Seyfarth (168).

In these conditions it is clear that we are not dealing with a primary infection in the organ but with a reaction between substances produced in an organism from an infection and some substance of an antibody nature. The reaction produced between the two substances is therefore to be considered the causal factor in destruction of the germinal elements. Since the marked inflammatory reaction occurs within such a short time it appears that we may have to deal again with a temperature factor.

VIII. TESTICULAR REACTIONS UNDER OTHER CONDITIONS

Sickness. It has been known at least since 1882 that often the testes become aspermatic in certain types of illness whereas in other types, even chronic conditions, the spermatogenetic function may continue unimpaired. Busch (32) reported on the spermatozoon condition of the testes of one hundred autopsy cases. In all cases of sudden death, whether through accident or suicide, the testes were found to contain spermatozoa. In acute cases (not over four weeks duration of sickness) 15 per cent showed a lack of

spermatozoa, whereas in longer sicknesses (complicated pulmonary infections, pneumonia, etc.), 31 per cent of cases lacked spermatozoa in the testes. Hansemann (68) studied the testis of human autopsy cases and determined that often the testes have been deprived entirely or partially of the germinal portion following pneumonia and typhus fever; in tuberculosis certain lesions may produce localized destruction but in the unimpaired portions spermatogenesis has continued. Cordes (38) examined the testes from human autopsies after common diseases such as pneumonia, scarlatina, peritonitis, meningitis, etc. Many of those dead of relatively rapid pneumonia or other febrile conditions lacked spermatozoa but retained a fairly well defined germinal epithelium. In general, the longer duration of the common diseases was accompanied by the greater testicular degeneration; in many cases there was complete loss of the germinal cell line with the possible exception of a few scattered spermatogonia. Mills (110) and Wolbach (211) studied testes obtained from autopsy of army recruits dead in camp from influenza and pneumonia. Mills in particular follows out as closely as he was able the correspondence of the testicular condition and the type of affliction; many of the cases were complicated with measles, epidemic influenza, etc. but he states that "roughly the severity of the injury corresponds directly with the duration of the pneumonia as closely as with any other single variable factor." The injury noted consisted of the disappearance of various cells in the epithelium of the seminiferous tubules, sloughing of the epithelium into the lumen with cellular destruction, and in more severe cases all germinal cells except spermatogonia had been removed from the tubules. Mills makes a futile attempt to correlate the different types of

degeneration with a common cause such as pure infections, complications, duration of infection, or with the infectious organism involved, and comes to the conclusion that "In the absence of definitive evidence to the contrary, the cause is assumed to be circulating toxins"

At the time of this writing the effects of higher temperatures in causing rapid degeneration of a similar nature in perfectly healthy testes was not known. It appears highly probable, from our experiments with higher temperatures, that the mere febrile condition alone is sufficient to produce all the types and grades of degeneration described. This appears all the more probable in view of the close correlation between the duration and the state of degeneration; rapidly fatal infections are in general correlated with testicular injury of a lesser grade than in more prolonged sicknesses. It is believed that this common explanation (high temperatures) for so many different cases of germinal epithelium destruction can be invoked here as the real cause of testicular degeneration following febrile sickness. It is well known that patients recovering from severe and prolonged fevers of different kinds are not rendered permanently sterile. This is in keeping with the general findings that where spermatogonial cells survive the destructive effects, complete regeneration of the testes follow.

Alcohol. It has been shown in many cases that the germinal tissue of the testicle of man and experimental animals is very susceptible to injury by alcohol when no perceptible injury is detectable in other organs of the body. Busch (32) noted that confirmed drunkards often showed a diminished amount of spermatozoa or an entire absence of them, particularly so when alcoholism was accompanied by cirrhosis of the liver. Simmonds (170) found an azoospermic condition one

hundred and twenty-five times among one thousand human autopsies. Of this number 7 per cent were cancerous, 14 per cent afflicted with chronic nervous disturbances, 18 per cent with phthisis, and 60 per cent were chronic alcoholics. He determined that among all autopsied human males there was a greater number sterile from the use of alcohol than from venereal diseases. Bertholet (16), and Weichselbaum and Kyrle (200) likewise show that testes of chronic alcoholics are degenerate; histologically different grades of injury have been illustrated by the latter writers. Degeneration from the use of alcohol is quite similar to the type found after elevation of temperature; spermatocytes and spermatids are often found loose in the lumen of the seminiferous tubule undergoing degeneration. Other tubules have been described as consisting of a vacuolated epithelium apparently caused by degeneration and liquefaction of cells locally in the meshes of the Sertoli reticulum. More severe injury involves all germinal cells with the exception of a few spermatogonia. Bertholet found that only two men out of thirty-nine habitual drunkards autopsied failed to show some degree of testicular degeneration.

The interstitial cells in alcoholic degeneration have been described as hypertrophied and in some cases as little changed. In general the testes are somewhat more firm and usually slightly smaller than normal. The seminiferous tubules are often of smaller diameter than normal ones.

Bouin and Garner (26), Arlitt and Wells (5), Allen (3) and Kostitch (79) have determined that feeding alcohol to normal rats causes the testes to show degeneration changes. There is a general agreement among these writers that degeneration follows in the reverse order

of production of the different elements of the germinal line; thus spermatozoa are often absent from testes that contain a fairly normal germinal epithelium. More severe injury is to be associated with both a sloughing of the spermatocytes and spermatids into the lumen, or a local cytolysis in situ and the consequent vacuolated condition of the Sertoli syncytium. The usual condition, perhaps, is to find some spermatogonia that apparently have not been affected.

With experimental alcoholism, as in chronic alcoholism in the human, the interstitial tissue is reported both as greatly hypertrophied and as practically normal.

Under the influence of alcohol, therefore, we find testicular degeneration of similar grades to those effected by high temperatures. It is a question whether there is any relation between the action of the causal agents in the two conditions but each serves to emphasize the labile nature of the cells of the reproductive line. The possibility of regeneration from uninjured spermatogonia is likewise common to the two conditions.

Dietary deficiencies. Allen (3) studied the testes of albino rats reared on a diet deficient in the water soluble vitamins (Osborne and Mendel). Rats that were otherwise normal had experienced degeneration of their germinal tissues. A usual condition was to find an entire lack of spermatozoa but in some of the animals the effects had been so severe that all cells of the germinal line have been reported absent, the seminiferous tubules containing only the Sertoli reticulum. At times the interstitial tissue was increased and in other testes approximately normal.

Mason (107) studied the testes of white rats after feeding with a basic diet sufficient to maintain a normal growth curve and good health of the colony. After the

attainment of sexual maturity male rats fed on the diet experienced a progressive degeneration of the germinal tissues. Spermatozoa were the first cells affected and these were followed in turn by spermatids and spermatocytes. Usually the spermatogonia were retained along with the Sertoli tissue. The interstitial cells appeared to remain normal. When to the stock diet, a small amount of lettuce was added the testes were unaffected. Mason considers the cause of degeneration to be a lack of Vitamine X (Evans and Bishop). He states that recovery from degeneration does not follow within seventy-five days after placing the animals on a normal diet. If spermatogonia are present, however, and uninjured, it would appear from other considerations that recovery should follow on return to normal diets.

We see therefore that the testis, in reference to its germ cell differentiating capacity, is an extremely sensitive organ. Many other conditions, not considered here, would only serve to emphasize its labile nature. There is yet much to be learned in its biology but it is evident that considerable progress has been made. Cross currents in the advance of our knowledge concerning the gametogenetic function are confusing but having considered a few of the major trends in this advancement we now come to consider the testis as an organ of internal secretion.

IX. INTERNAL SECRETION OF THE TESTIS

General considerations. It has been thoroughly appreciated for centuries that removal of the testicle from man or animals has an effect upon the entire organism. The present day custom of castrating domestic animals is an old one, and the Eunuch is referred to in biblical literature. It is clear that in general the testicle exerts some influence upon the character of the animal that leads to the

production of a more or less well defined masculine type. In domestic animals this is at times indicated by characteristic body form; in some ruminants horn growth is a specific male character. In man body form is not always clearly indicative of masculinity, but certain skeletal structures such as the pelvis is usually quite specific in form; growth of the larynx and the attendant coarseness of voice is relatively diagnostic; hair tracts on the body of man differ to some extent from those of woman, and within somewhat narrower limits the growth of beard and mustache on the face. The entire accessory organs of reproduction in the male are dependent upon the testis for their complete development; penis, seminal vesicles (where present) vas deferens, and prostate remain characteristically infantile when the testes have been removed at an early period in life. In both man and animals testis removal has been held to favor growth in length of the long bones (69, 141, 167, 186) due to delay in ossification of the epiphyses; many cases of overgrowth of bones following castration have been reported but in the guinea pig such differences if present at all are minimal (117). Finally the psychic nature or the attitude of the male to the female in both man and animals appears to be quite largely conditioned by the sex glands, though it appears to be a question whether they are wholly dependent upon testicular influences. It may be suggested that in attempting to define the testicular influence upon both somatic and psychological characteristics many writers have allowed their ardor to carry them into dangerous territory and have added confusion to the problems rather than restoring order.

Steinach (177 to 183) in his celebrated work of hormone analysis in rats and guinea pigs has used as indicators of,

masculinity certain types of hair coat, fat deposition, size, weight, and the psychological nature. Moore (112, 115, 116, 117) has criticised these criteria on the grounds that they are not sufficiently diagnostic to enable one to choose between normal males and females in a mixed colony, and are therefore questionable indicators of sex. Such characters as are not sufficiently well defined or characteristic are dangerous implements with which to attempt to advance our knowledge of the internal secretion of the sex glands.

Such misleading applications of questionable indices is nowhere more apparent than in the clinical literature concerning sex and the effects of supposedly remedial operations such as vasectomy and testis transplantation. For the purpose, one may assume that a man of fifty-five to sixty years of age is prematurely senile due to slowing down of the activity of his sexual apparatus; cases are on record where lack of spermatozoa in the semen is considered adequate proof of senility. Under these conditions hospitalization embodying rest and excellent care, combined with a vas deferens ligation, or a testis transplantation, and plenty of suggestion and anticipation, have produced most remarkable results particularly in reference to the reassumption of sex inclinations; spermatozoa may again be found in the semen. Busch (32) in 1882 points out that men of eighty years may possess functional testes producing spermatozoa and likewise men above ninety years. Many conditions may lead to a temporary azoospermia but as long as spermatogonia remain capable of activity the entire seminal line can undoubtedly be restored if the unfavorable causes, whether mental or physical, be removed. Rest, good care and psychology work wonders along with, perhaps, a harmless operation, but the operation is all too often credited with the entire improvement.

Castration in man undoubtedly has a great psychological effect upon the individual but certain observations if rightly considered should temper our conclusions that the entire psychological reaction is conditioned by substances poured into the body from a testis or a graft. In 1801 Sir Astley Cooper (39) removed the second testis from a man semicastrated two years earlier. Cooper following this case for twenty-nine years, reports the patient experiencing an emission on the third night after operation. Similar observations have been reported following testis transplantation with the implications that the effects of the testis transplant have this early become detectable. During the first year after total castration Cooper's patient experienced emissions in coitus. Two years after operation erections were strong but relatively transient. A general decline was noted, but twenty-eight years after the removal of both testes erections were experienced as well as erotic dreams and sensations of emissions. It is likewise instructive to follow the reports on the psychological nature of the Skopecs studied by Tandler and Grosz (186, 187, 188). This religious sect, practicing castration of young males, are in general of two types: one grows to excessive height and are lean individuals whereas the second is characterized by excessive fat deposition. The voice is characteristically boyish and it is well known that many famous male choirs and soloists are individuals castrated for the purpose of producing a voice of a particular caliber. These Skopecs, according to Tandler and Grosz, appear to be a long lived group of people, which would appear to minimize the contentions of certain rejuvenation advocates that the life of an animal can be prolonged by vasectomy or testis transplantation. Like Cooper, Tandler and Grosz maintain that sexual desire is not entirely abolished by total castration.

They report one individual totally castrated for twenty-one years, as exercising coitus almost daily and with slight emissions. Erections were strong but not greatly prolonged. It is likewise reported that those upon whom the "Great operation" had been done (removal of both testes and penis) often find pleasureable associations with females and actually experience a type of sexual orgasm.

From such considerations, therefore, it would appear that conclusions from operation on men have not always been stated with caution and much of the literature dealing with the effects of sex gland manipulations cannot be highly regarded.

Work on the effectiveness of sex glands in the experimental animal is likewise often misleading because of a lack of appreciation of the limitations of indices employed to grade the effectiveness. It is usually considered that a male animal shows no inclination towards females after the removal of its testes, but Moore (116) reported castrated male guinea pigs carrying ovarian grafts sufficiently effective to modify the mammae of the male, still acting strongly the part of the male. Indeed he has observed male guinea pigs castrated at thirty days of age that continued to show strong male reactions in the presence of females for sixteen months; the male sex call, pursuit and attempts at mounting the female were so positive that the animal was employed as a test animal to detect females in heat.

Source of the internal secretion. Admitted that the testis does exercise an influence upon the organism that results in the production of the specific male characteristics, the attention of many workers has been directed toward the localization of the source of such an internal secretion.

The work of Berthold (17) gives a starting point in such analyses. He determined in the bird that the testis

could prevent the animal from becoming a capon after its removal from the normal to a foreign position if it became vascularized and persisted; the testis placed in the abdomen and supplied by blood vessels from the intestine kept the cock normal for some months whereas complete removal produced a capon. He believed the active principle involved was a substance liberated into the blood stream that exerted a gradual influence over the entire body and that nervous transmission from the testes was not involved.

It was perhaps logical to consider that the generative portion of the testis was responsible for the production and maintenance of the secondary sex characters as well as for the production of mature germ cells. Brown-Sequard (31) on the assumption that an active functional testis was responsible for the health and vigor of the young, injected subcutaneously into himself an extract made from the young testis of dogs and rabbits. At the beginning, a very feeble old man, he believed that he derived great benefits from such injections. He maintained that his muscular strength, vitality and youthful ire were stimulated and that he was able to continue his scientific work for many years longer than he otherwise would have been capable.

It was appreciated long before this time, however, that man and animals with undescended testes retained their virility despite the consequent sterility (Goubaux and Follin (57), Godard (54), Monod and Arthaud (111)). Griffiths (59) is remarkably clear in calling attention to the fact that the general influence of the testis on the animal is entirely independent of its spermatozoon producing capacity.

Leydig (86), in his comparative anatomy studies on the different mammalian testes, described for the first time certain

large cells containing fatty spherules and pigment, as a constant occurrence in the connective tissue stroma between the seminiferous tubules. The significance of these cells, commonly known as the interstitial cells of Leydig has been a point of contention for many decades (Jacobson, Lubarsch, Reinke, Stieda, Plato, von Lenhossek, Bouin and Ancel, Felizet and Braca, Regaud and Policard, etc.). These cells have been studied in a large number of mammals and though a constant feature of the testis they have been found to vary greatly in amount, distribution, and types of cellular inclusions. They appear in relatively large quantities in the embryonic testis, in apparently diminished quantities as the testis develops, but present throughout life, and again somewhat more numerous in an old animal, or man (Plato, Bouin and Ancel, Kasai, Allen, Whitehead).

Among the older writers some were of the opinion that the interstitial cells represented merely an embryonic rudiment left in the testis during its formation and had no other significance, but later workers came to view the elements as modified connective tissue cells having some particular functional significance. Von Ebner observed that the enclosed pigment was more pronounced in older than in younger animals. Jacobson (76) noted that in pathological conditions the interstitial cells were apparently increased in amount while Hanseinnann (68), in the hibernating marmot, noted that Leydig cells were not in evidence but that two months after hibernation the testis presented the picture of a sarcoma due to the tremendous increase in the amount of Leydig cells; under pathological conditions, likewise, he noted great variation in the amount of these cells.

In attempting to determine the significance of the interstitial cells the current

ideas of the time centered around the conception of the Leydig cells as a trophic organ responsible for the nutritional requirements of the generative tissue of the testicle. Plato (139, 140) representing this type of opinion, believed that these cells, located between the blood vessels and the seminiferous tubules, extracted materials from the circulation, elaborated the fat and pigment (which in general he considers only different phases of the same process) and passed these substances through the basement membrane into the seminiferous tubules where he attempted to trace their distribution from the Sertoli cells to the different cells of the germinal line. He figures small canaliculi through the basement membrane containing a stream of the elaborated material from Leydig cells into the tubules.

A year earlier Reinke (150) described elongated, blunt, crystalloid rods in the interstitial cells of a tuberculous human testicle. These he found in normal human testes from the fifteenth to the sixty-fifth year and believed they represented the elaborated products of the cells. He believed the Leydig cells secreted these bodies and from materials detected in the lymphatics concluded that the materials were discharged into these channels, mildly suggesting that they might represent a product having to do with the sexual ardor of the male.

Many different inclusions such as acidophile and basophile granules, crystalloids, fatty spherules, different pigments and other types of stained materials have been described from different mammalian testes and at least until 1903 the general opinion was held that these substances represented the secreted products destined for nutrition of the seminal portion of the testis.

In 1903 Bouin and Ancel after an elaborate histological, cytological and experimental group of researches brought

forward a new point of view regarding the significance of the interstitial cells that has stimulated renewed interest in the entire field of sexual biology. Their own detailed cytological studies (22) and those of their predecessors appeared to establish beyond all doubt that the interstitial cells were glandular in nature and function. Admitting, with many of their colleagues and predecessors, the probability that the secretion products of these cells were nutritive substances for the germinal cells, they believed that all of it was not so utilized and that fundamentally the interstitial portion and the generative portion of the testis are independent tissues. They point out: (1) that the interstitial cells are to be found in intensive secretory activity long before the activity of the germinal portion is initiated. (2) This interstitial tissue is present throughout life in all mammals, and is of a common secretory type though differing in minor details as to inclusions. (3) After the germinal portion has ceased to be active in old animals the interstitial cells continue to secrete. (4) They believe that the primary distribution of the Leydig cells is around blood vessels rather than in close opposition to the basement membrane of the tubules. They trace secretory products discharged into the lymphatics rather than into the seminiferous tubules. (5) In cryptorchid testes there is no germinal tissue whereas Leydig cells are present in an overabundance and actively secreting. (6) After certain diseases the generative portion has suffered degeneration but interstitial cells are retained and are actively secreting. (7) They maintain that occluding the vas deferens causes a loss of all the generative portion of the testis but a retention, perhaps an increase, of interstitial tissue.

From these and other considerations they argue that since there is no inter-

dependence between the interstitial tissue and the germinal tissue, and that since an animal may lose all its generative portion without showing any signs of castration, there must be other tissues in the testis than the germinal line that are responsible for the maintenance of the secondary sex characters. Their histological and cytological studies failed to show any secretory activity in portions of the testis other than the interstitial cells and they therefore conclude that the interstitial cells manufacture a substance that is poured into the general circulation—and internal secretion—which is responsible not only for the production of the secondary sex characteristics but at the same time for their maintenance; the aggregate features of maleness are therefore conditioned by the secretions from interstitial cells alone and this function is separate from, and independent of, the production of germ cells. We now know that their conception of the effects of vas deferens occlusion were wrong (see section III) but the fact remains that by whatever means the condition is brought about, an animal will retain its morphological secondary sex characteristics and its sexual ardor in the absence of at least all cells of the germinal line with the possible exception of spermatogonia.

The internal secretory activity of the interstitial cells had been mildly suggested by earlier workers (Reinke (190), Regau and Policard (149)) but it remained for Bouin and Ancel to develop the idea into a well formed hypothesis. Extending the conception by experimental and morphological studies (24, 25) they have attempted to correlate the amount of interstitial tissue with graded sex differentiation. Thus by removal of a normal testis from the pig, with one testis retained in the abdomen, they believed it demonstrated that the interstitial tissue

of the remaining testis undergoes a compensatory hypertrophy—an approximate doubling in amount of interstitial tissue—to restore the loss conditioned by removal of the descended testis. In cryptorchid pigs they make an attempt to correlate degrees of differentiation of the reproductive system and the interstitial cell content of the testes. They, furthermore, carry the conception to the extent of making the interstitial cells responsible for the determination of the sex of the primordial germ cells.

A tremendous stimulus to the conception of the interstitial tissue as the internal secretory portion of the testis was given six years later by Steinach (177 to 183). The work also of Sand (157 to 164) and Lipschutz and his students (91 to 95) has added a great deal of confirmatory evidence and new observations.

Steinach studied principally the effects of castration and subsequent gonad transplantation in both sexes of the rat and guinea pig, and the effects of ligation of the vas deferens in the male. He showed that castrated males in which testis grafts had been growing retained all their secondary sex characters instead of reverting to merely castrated animals. Since the graft tissue consisted primarily of Leydig cells he considers these to be the source of the sex hormones; these cells were not only retained but were believed to have undergone a compensatory hypertrophy. The seminiferous tubules were always degenerate and contained only the Sertoli reticulum; cells of the generative line were always lacking. Similarly, in ligating the vas deferens, Steinach reported that the generative portion suffered degeneration and in some manner the operation stimulated increased development of Leydig cells. These cells, believed thus to produce an excess of hormone, were then indirectly responsible

for stimulating the entire organism and, according to his account, the testes of senile animals previously devoid of germ cells would again become active and a renewed germinal cell activity would follow. The animal was believed to have been rejuvenated, thus becoming a younger animal in all its characteristics. Such operations, largely due to Steinach's reports, are now being employed as remedial measures both on experimental animals and on man (Steinach (183) Sand (163), Benjamin (12)). The experimental work of Sand is largely confirmative of Bouin and Ancel and Steinach. He maintains, with Bouin and Ancel, that unilateral castration causes compensatory hypertrophy of Leydig cells in (experimental) cryptorchid testes.

The experimental work of these biologists stimulated anew the study of the histological structure of Leydig cells with attempts to find the specific secretory products. Whitehead (202 to 208) has described many types of apparent secretory products in Leydig cells of different mammals. Fatty granules or vacuoles appear in most testes but in a few the fatty material is almost wholly absent. Pigment materials of many varieties have been noted and granules of a protein nature as well as crystalloids have again been brought to our attention. Wagner (197) has recently reviewed the literature and added observations to this field of work. He is convinced that the cells are secretory and that the products can be traced into the lymphatics; he believes the individual cell is not destroyed in liberating the secretory products (see also Cejka (34)).

Added correlation between hormones and interstitial cells is found in the study of the free-martin by Lillie and his students (88, 89, 90, 7, 36, 210). The free-martin (a female calf cotwin with a

male) is modified sexually when by a fusion of the embryonic membranes an intermixture of blood, from the male and the female in utero, is permitted. The effective modification is detectable at an early stage and has been found to be effective just after the appearance of Leydig cells in the embryonic testis (Lillie and Bascom (90) Bascom (7)). The effectiveness of the modification is so great that a determined female may be caused to produce testes out of undifferentiated ovaries (Lillie, Chapin, Willier, Bissonnette).

Thus there has developed a relatively strong case in favor of the interstitial cells as the source of the internal secretion, or hormone, of the mammalian testis (the case is somewhat similar in other vertebrates). But if we examine critically the main points of contention it will become apparent that the question is by no means definitely settled.

1. The experiments on vas deferens ligation (see section III) from the morphological side may now be ruled out. It has been bountifully shown that occlusion of the vas deferens in the dog, guinea pig, rat, rabbit, sheep, cat, pig and man causes neither degeneration of the generative portion of the testis nor hypertrophy of the interstitial cells. What, then, of rejuvenation by this means (Steinach, Sand, Haire, Schmidt, Benjamin)?

The criteria employed in experimental animals are of such a nature and so variable among individuals as a whole that it is capable (by selection) of being applied either for or against the hypothesis; and certainly it is selection to choose two positive cases of degeneration as against thirteen negative cases and yet hold that the operation gives positive effects (159). Among animals there may appear certain lassitude, loss of hair, sex disinclination, loss of weight and combative ability in old age but it is not so clear that such condi-

tions are due to lack of sex hormones. This is all the more confusing for the hypothesis when so many have stated that interstitial cells are much more abundant in testes of old animals and man. The same decrepit indicators occur many times in males, of animal colonics with both testes present, that are much younger than the average sex life of the animal. Good care and particular attention often restores such animals to sleek coated vigorous animals. In short, nutritional disturbances, parasitism, and general infection may produce these symptoms. Steinach himself has discussed the inherent difficulties of properly judging an animal a fit candidate for rejuvenation. In man, likewise, some of the most remarkable effects of rejuvenation through vas deferens ligation have been reported on individuals under fifty years of age (see Haire (63), Schmidt (166)) whereas many men are sexually active for much longer periods (see Busch '82). It is merely granting an assumption to accept the statement that such individuals are prematurely senile due to a diminution of their testicular secretions. No one has yet proven that an individual castrated early in life is shorter-lived or more decrepit than a man in possession of his testes. Indeed Tandler and Grosz (187, 188) maintain that the Skopecs are a long-lived group of people.

It is unnecessary to enter into a discussion of the effects of suggestion and psychology in general, on matters relating to sex in the human individual. It is a condition of mental attitude which in our modern civilization is useless as a qualitative or quantitative indicator of effectiveness of operative procedures (see section IV). Vasectomy, as a remedial, rejuvenating procedure has failed to justify its utilization. Moreover the very basis of the conception has been proven false.

2. Compensatory hypertrophy of the

interstitial cells has been one of the chief objective conditions that has led to the contention that in this tissue resides the source of the internal secretions of the testis. Bouin and Ancel note an apparent doubling of this tissue in a unilateral cryptorchid testis if the opposite one had been removed earlier. They believe this increase compensated for that lost in removal. Steinach claims that hypertrophy occurs in all testis grafts. Practically all writers on cryptorchid tests maintain that this tissue has been increased. We may therefore inquire, first, whether compensation is necessary and the tissue reactions of any significance from the internal secretory viewpoint and, second, whether there is an actual hypertrophy of the Leydig cells.

It is well known that the loss of one testis leads to no diminution of the secondary sexual characteristics in animals or man. Despite the contentions of earlier writers that a single remaining testis does become larger than normal Lipschutz (92) holds that attainment of ultimate size is only more rapid and that in the end neither generative nor interstitial parts are in any way increased above the normal. Furthermore Lipschutz and his coworkers (95) have proven that 1 per cent of the normal testicular mass is sufficient to maintain all the secondary sexual characteristics. These facts lead one to question the significance usually attributed to the compensatory hypertrophy where such a condition actually follows in single or double cryptorchid testes. If 1 per cent of the normal testicular mass is all sufficient for the animals' need, of what significance is interstitial cell hypertrophy *in each of two complete testes that have remained in the abdomen?*

Hypertrophy of Leydig cells has been held to exist in cryptorchid testes, cases of obliterated vas deferens, testis grafts,

after X-ray treatment, excessive temperatures, use of alcohol (chronic or experimental), diseases of many kinds, dietary deficiencies and other conditions. Can such conditions have any significance for the internal secretory needs of the animal? Is it really true that hypertrophy occurs? In brief, practically any condition leading to loss of the generative cells is accompanied by apparent Leydig cell hypertrophy. This may be true for the testis as a whole or minor local portions of it (Kyrle (82)), yet these cells are rarely noted in mitosis. When the germinal epithelium is lost from the seminiferous tubules these latter characteristically decrease in size (122). With a decrease in diameter of the tubules the testis as a whole becomes appreciably smaller and if there were actually no increase in the number of Leydig cells they would naturally be restricted to a smaller area and thus exist, *relative to number of tubules*, in an overabundance. In a given microscopic field therefore, there would be a great increase in Leydig cells. Determination of hypertrophy has been made in this manner and it must be emphasized that a quantitative increase in a given microscopic field is no criterion of the actual content in the entire organ. This question has been discussed in another place (Moore (122)) and it is considered that compensatory hypertrophy not only does not exist but also that any slight increase in number or size of Leydig cells loses its significance as being a quantitative indicator of the internal secretion of the organ. Quantitative methods carefully employed should be a great factor in settling the present controversy of compensatory hypertrophy of the cells of Leydig. The commendable attempt of Bascom (8) will undoubtedly give us much more exact information than has hitherto been available. In contrast to Bouin and

Ancel, Hanes, and Sand, Bascom, using his quantitative method, maintains that there is not an hypertrophy of Leydig cells in unilateral cryptorchid testes after removal of the opposite one.

In testis grafts, contrary to Steinach and Sand, it has been found that, more often than not, there is a lack of apparent hypertrophy of the Leydig cells (Moore (125)). Apparent increases may occur in these grafts but it occurs just as readily in grafts residing in normal females, where with both ovaries present there cannot be a question of the need of increased secretion, as in castrated males. Such increases were found without any definite relation to any secretory need or sexual condition of the host animal. In castrated males, for example, grafts may show large interstitial areas, one graft revealing a large group of typical Leydig cells and another relatively devoid of them, having instead ordinary connective tissue cells between the tubules. It cannot, therefore, be accepted in principle that Leydig cells undergo hypertrophy in testis grafts.

3. The seasonal cycle of the testes shown by some hibernating animals breeding but one a year reveals striking changes in the different tissue of these organs. Hansemann (68) observed that the hibernating marmot had only slight amounts of connective tissue between the seminiferous tubules and no typical Leydig cells; spermatogenesis was in abeyance. Two months after the awakening period, in the height of its breeding season, Leydig cells were so large and numerous as to give to the testis the appearance of a large-celled sarcoma. Could it be that their activity here was definitely responsible for the occurrence of the seasonal cycle? Ganfini (52a) stated that Leydig cells were not absent from the testes of this animal but were only much

smaller during hibernation. Regaud (144) found in the mole a different relationship of the testis elements; active spermatogenesis was not accompanied by interstitial cell hypertrophy. After the breeding season the interstitial cells become maximal and so remain after the disappearance of the generative portion; this is subsequent to the breeding season. Tandler and Grosz (189) likewise note that the testes of the breeding mole have few interstitial cells. As the generative portion recedes to its minimum development the interstitial cells hypertrophy to their maximum development and staining ability. In the hedgehog Marshall (104) finds a correlation between maximal interstitial cell development and testicular activity whereas Rasmussen (142) in the woodchuck finds that interstitial cell increase follows considerably behind that of generative tissue activity. When the reproductive portion is again at its minimum state of activity the interstitial cells are maximal. It is seen, therefore, that no definite correspondence is to be found between the interstitial cell activity and the breeding period or the process of gametogenesis. Two hibernating mammals may be entirely opposite in the relationship between increase of Leydig cells and the reproductive activity.

In conclusion one is impressed with the conflicting opinions and lines of evidence relating to interstitial cell activity and the internal secretory function of the testis. The features most impressive to Bouin and Ancel, Steinach and others appear to be open to decided question, and, for many of their opinions there now appears to be a different explanation. Leydig cells in their formation and their increase in testicular changes are apparently ordinary connective tissue cells that have undergone a change (Plato, Bouin and Ancel, Allen, Whitehead, Hofmeister, Kasai,

Sand, Moore, Oslund, Kyrle, Rasmussen, Wagner and others); few modern writers hold the old conception that they are epithelial in origin. When the generative portion suffers a decline the interstitial cells become prominent and when regeneration occurs these appear to return to the ordinary connective tissue state. In other terms, there appears to be somewhat of a balanced relationship between the Leydig cells and the generative portion, perhaps harking back to the nutritional viewpoint initiated by Plato and substantiated more recently by Kyrle. The so-called compensatory hypertrophy appears to be a reaction of the tissues to local or general disturbances in the organ (Moore) rather than having any significance to increased secretory needs of the organism.

When one appreciates the normal quantity and distribution of the Leydig cells in the testes of different mammals, and its variability in the same animal, it becomes difficult to appreciate its significance as a secretory organ. Normally the pig has great quantities of Leydig cells, the horse to a less extent, the cat and others, whereas in the sheep they are scarcely to be found. The dog, most rodents and man have a small quantity in comparison with other mammals. No satisfactory explanation of the secretory need appears

to offer a suggestion for these discrepancies.

In general there appears a decline from the pinnacle to which the significance of the interstitial cells has been elevated in the last score of years and at present there are those who strongly proclaim that such cells have absolutely nothing to do with determining or sustaining the secondary sexual characteristics (Brack '22, Cejka '23 and others). Other tissues of the organ have in turn come in for discussion as the probable source of the internal secretions; the generative portion, some cells of which almost invariably remain after degeneration and appear capable of activity, and the vast Sertoli reticulum, are usually retained in the organ. Discussion of these, however, will not settle the problem and already this account is perhaps too long, though considerably incomplete for an exhaustive discussion of the biology of this organ. Many phases of the tissue reactions as well as the internal secretion question have had to be omitted. It should be clear, however, that the problems pertaining to the mammalian testis are by no means exhausted. Many aspects of both major problems are decidedly open to question, and many particulars await solution but it is certain that the advances of the last half century have been tremendous.

LITERATURE LIST

- (1) ALBERS-SCHÖNBERG. 1903. Ueber eine bisher unbekannte Wirkung der Röntgenstrahlen auf den Organismus der Tiere. Münch. Med. Wochenschr., 50: 1859-1860.
- (2) ALLEN, B. M. 1904. The embryonic development of the ovary and testis of the mammals. Amer. Jour. Anat., 3: 89-134.
- (3) ALLEN, EZRA. 1919. Degeneration in the albino rat testis due to a diet deficient in the water soluble vitamine, with a comparison of similar degeneration in rats differently treated and a consideration of the Sertoli tissue. Anat. Record, 16: 93-112.
- (4) ANGEL AND BOVIN. 1923. Les cellules séminales ont-elles une action sur les caractères sexuelles? C. R. Soc. Biol., 89: 175-178.
- (5) ARMITT, ADA H. AND H. G. WELLS. 1917. The effect of alcohol on the reproductive tissues. Jour. Exp. Med., 26: 769-778.
- (6) BAILEY AND MILLER. 1921. Text-book of Embryology. Wm. Wood and Co. New York.
- (7) BASCOM, K. F. 1923. The interstitial cells of the gonads of cattle, with especial reference to their embryonic development and significance. Amer. Jour. Anat., 31: 223-259.

- (8) BASCOM, K. F. 1925. Quantitative studies of the testis. Some observations on the cryptorchid testes of sheep and swine. *Anat. Record*, 30: 225-241.
- (9) BASSO, G. L. 1906. Ueber Ovarientransplantation. *Arch. f. Gynäk.*, 77: 51-62.
- (10) BELFIELD, W. T. 1924. Some phases of rejuvenation. *Jour. Amer. Med. Assn.*, 82: 1237-1242.
- (11) BENEDICT AND SLACK. 1911. A comparative study of temperature fluctuation in different parts of the human body. *Carnegie Publications* no 155.
- (12) BENJAMIN, H. 1922. The Steinach operation: report of twenty-two cases with endocrine interpretation. *Endocrinology*, 6: 776-786.
- (13) BERGOINE, J., AND TRIBONDEAU. 1904. Action des rayons X sur les spermatozoïdes L'Homme. *C. R. Soc. Biol.*, 57: 595-596.
- (14) ———. 1904. Action des rayons X sur le testicule du rat blanc. *C. R. Soc. Biol.*, 57: 154-158, 400-402, 592-595.
- (15) ———. 1905. Aspermatogenese expérimentale après une seule exposition aux rayons X. (and other papers). *C. R. Soc. Biol.*, 58: 282-284, 678-680, 1029-1031.
- (16) BERTHOLET, ED. 1909. Ueber Atrophie des Hodens bei chronischem Alkoholismus. *Centr'bl all. Path.*, 20: 1062-1066.
- (17) BERTHOLD. 1849. Transplantation der Hoden. *Arch. f. Anat. u. Physiol.*, p. 42.
- (18) BEVAN, A. D. 1918. Undescended testes. *Surgical clinics of Chicago*, 2: 1101-1117.
- (19) BISSONNETTE, T. H. 1924. The development of the reproductive ducts and canals in the free-martin with comparison of the normal. *Amer. Jour. Anat.* 33: 267-346.
- (20) BLAND-SUTTON, J. 1910. The value of the undescended testis. *The Practitioner*, 84: 19-30.
- (21) BORN. 1921. *Revue Scientifique* no. 6.
- (22) BOUTIN AND ANCEL. 1903. Recherches sur les cellules interstitielles du testicule des mammifères. *Arch. de Zool. Exp. et Gen.*, 4th. ser., 1: 437-522.
- (23) ———. 1904. Sur la ligature des canaux déferents chez les animaux jeunes. *C. R. Soc. Biol.*, 56: 84-86.
- (24) ———. 1904. Recherches sur la signification physiologique de la glande interstitielle du testicule des mammifères I. Role de la glande interstitielle les individus adultes. *Jour. de Physiol.*, 6: 1012-1022.
- (25) ———. 1904. II. Role de la glande interstitielle chez l'embryon, les sujets jeunes et âgés; ses variations fonctionnelles. *Jour. de Physiol.*, 6: 1039-1050.
- (26) BOUTIN AND GARNIER. 1900. Alterations du tube séminifère au cours de L'alcoolisme expérimental chez le rat blanc. *C. R. Soc. Biol.*, 52: 23-25.
- (27) BRACK, E. 1921. Ueber innere männliche genital Missbildungen bei einseitiger Nierenaplasie. *Zeitschr. f. Urologie* 15. (not seen in original).
- (28) ———. 1922. Zur pathologischen Anatomie der Leydigzelle. *Virchow's Arch. f. Path. Anat. u. Physiol.*, 240: 127-145.
- (29) BRISSAUD, E. 1880. Sur les effets de la ligature du canal déferent. *Arch. de Physiol.*, 2nd. ser., 7: 769-789.
- (30) BROWN, F. T. AND A. T. OGDON. 1905. X-rays and sterility. *Amer. Jour. Surgery*, 18: 179-182 (not seen in original).
- (31) BROWN-SQUARD. 1889. Expérience démontrant la puissance dynamogénique chez L'homme d'un liquide, extrait le testicules d'animaux. *Arch. de Physiol.*, 1 (ser. v): 651.
- (32) BUSCH, AUGUST. 1882. Ueber Azoospermie bei gesunden und kranken Menschen nebst einigen Bemerkungen zur pathologischen Histologie des menschlichen Hodens. *Zeitschr. f. Biol.*, 18: 496-521.
- (33) CASTLE, W. E. AND J. C. PHILLIPS. 1911. On germinal transplantation in Vertebrates. *Carnegie Inst. pub. no. 144.*
- (34) ČAJKA, BORUM. 1923. Eine Studie über die Genese und Funktion des Interstitiums auf Grund der Untersuchungen an seneszenten Hoden. *Arch. f. entw'mech.*, 98: 524-578.
- (35) CEVOLOTTO, G. 1909. Über verpflanzungen und Gefrierungen der Hoden. *Frank. Zeitschr. f. Path.*, 3: 331-337.
- (36) CHAPIN, CATHERINE L. 1917. A microscopic study of the reproductive system of foetal free-martins. *Jour. Exp. Zool.*, 23: 433-482.
- (37) CORBUS, B. C. AND V. J. O'CONNOR. 1922. The familial occurrence of [undescended testes. *Surgery, Gynecol. and Obstetr.*, 34: 237-240.
- (38) CORDS, H. 1898. Untersuchungen über den Einfluss acuter und chronischer Allgemeinerkrankungen auf die Testikel, speciell auf die Spermatogenese, sowie Beobachtungen über das Auftreten von Fett in den Hoden. *Virchow's arch.*, 151: 402-428.
- (39) COOPER, SIR ASTLEY. 1830. *Observations on the structure and diseases of the testis.* London. 1st. ed.

- (40) CORNER, E. M. 1904. The value of the imperfectly descended testis, the advisability of operation, and the value of the operations performed for its relief. *Brit. Med. Jour.*, 1: 1306-1309.
- (41) CREW, F. A. E. 1922. A suggestion as to the cause of the aspermatic condition of the imperfectly descended testis. *Jour., Anat. (Lond.)*, 56: 98-106.
- (42) CUNNINGHAM. 1917. *Text-book of Anatomy*. Wm. Wood. New York.
- (43) CUNNINGHAM, J. T. 1921. *Hormones and Heredity*. The Macmillan Company. New York.
- (44) DAVIS, D. M. 1924. *Pathological anatomy and histology of the testicle. Endocrinology and metabolism*. Appleton. New York, 2: 473-490.
- (45) FELIZET, G., AND A. BRANCA. 1898. *Histologie du testicule ectopique*. *Jour. de Anat. et Physiol.*, 34: 589-641.
- (46) ———. 1902. *Recherches sur le testicule en ectopie*. *Jour. de Anat. et Physiol.*, 38: 329-442.
- (47) FOA, C. 1901. *Sur la transplantation des testicules*. *Arch. Ital. de Biol.*, 35: 337-348.
- (48) FOOTE, A. 1898. *Zur Hodentransplantation bei Hahnen*. *Centr'bl f. Physiol.*, 12: 898-901.
- (49) FRIEDEN. 1903. *Hodenveränderung bei Tieren nach Röntgenbestrahlungen*. *Münch. Med. Wochenschr.*, 50: 2295.
- (50) FUKUI, N. 1923. On a hitherto unknown action of heat ray on testicles. *Japan Medical World*, 3.
- (51) ———. 1923. Action of body temperature on the testicle. *Japan Medical World*, 3.
- (52) ———. 1923. On the action of heat rays upon the testicle: An histological, hygienic and endocrinological study. *Acta Scholae Med. Univ. Imp. in Kito.*, 6 (fasc. 11): 225-258.
- (52A) GANFINT, C. 1903. *Les cellules interstitielles du testicule chez les animaux hibernants*. *Arch. Ital. de Biol.*, 40: 323-324.
- (53) GOSSELL, R. 1898. *Versuche über Transplantation des Hodens in die Bauchhöhle*. *Centr'bl f. All. Path. Anat.*, 9: 737-739.
- (54) GODARD, M. E. 1856. *Études sur la monorchidie et la cryptorchidie*. *C. R. Soc. Biol.*, 2nd ser., 3: 315-460.
- (55) GODDARD, T. R. 1920. Hypertrophy of interstitial tissue of the testis in man. *Jour. Anat. (Lond.)*, 54: 173-176.
- (56) GOSSELIN, L. 1847. *Memoire sur les obliterations de voies spermatique*. *Arch. Gen. de Med.*, 4th. Ser. 14: 405-424, 15: 40-52.
- (57) GOUBAUX, A. AND E. FOLLIN. 1855. *De la cryptorchidie chez l'homme et les prinapaux animaux domestiques*. *C. R. Soc. Biol.*, 2nd. ser., 2: 293-330.
- (58) GRIFFITHS, JOSEPH. 1893. The structural changes in the testicle of the dog when it is replaced within the abdominal cavity. *Jour. Anat. and Physiol. (Lond.)*, 27: 482-499.
- (59) ———. 1894. Retained testes in man and in the dog. *Jour. Anat. and Physiol. (Lond.)*, 28: 209-220.
- (60) ———. 1894. The condition of the testes and prostate gland in eunuchoid persons. *Jour. Anat. and Physiol. (Lond.)*, 28: 221-224.
- (61) ———. 1895. Three lectures on the testis. *The Lancet*, 1: 791-798, 916-920.
- (62) ———. 1896. The effects upon the testis of ligature of the spermatic artery, spermatic veins, and of both artery and veins. *Jour. Anat. and Physiol. (Lond.)*, 30: 81-105.
- (63) HAIRE, NORMAN. 1925. *Rejuvenation*. The MacMillan Company. New York.
- (64) HANAU, A. 1897. *Versuche über den Einfluss der Geschlechtsdrüsen auf die Secundären Sexualcharactere*. *Arch. f. d. Gesamte Physiol.*, 65: 516-517.
- (65) HANES, F. M. 1911. Relation of interstitial cells of Leydig to the production of an internal secretion by the mammalian testis. *Jour. Exp. Med.*, 13: 338-354.
- (66) HANES, F. M. AND J. ROSENBLUM. 1911. A histological and chemical study of the fatty matter of normal and cryptorchid testes. *Jour. Exp. Med.*, 13: 355-364.
- (67) HARVEY, W. G. 1908. On the pathological effects of Roentgen rays on animal tissues. *Jour. of Pathology*, 12: 549-556.
- (68) HANSELMANN, D. 1895. Ueber die sogenannten Zwischenzellen des Hodens und deren Bedeutung bei pathologischen Veränderungen. *Virchow's Arch.*, 142: 538-546.
- (69) HATAI, S. 1915. The growth of organs in the albino rat as affected by gonadectomy. *Jour. Exp. Zool.*, 18: 1-45.
- (70) HERLITZKA, A. 1900. *Recherches sur la transplantation, La transplantation des ovaires*. *Arch. Ital. de Biol.*, 34: 84-118.
- (71) HERXHEIMER, G., AND K. F. HOFFMANN. 1908. Ueber die anatomischen Wirkungen der Röntgenstrahlen auf den Hoden. *Deutsch. Med. Wochenschr.*, 34: 1551.

THE QUARTERLY REVIEW OF BIOLOGY

- (72) HEWBER, EVELYN E. 1916. The structure of the thymus gland and of the reproductive organs in white rats, together with some observations on the breeding capacity of these animals. *Jour. Physiol. (Lond.)*, 50: 434-458.
- (73) HOFMEISTER, F. 1872. Untersuchungen über die Zwischensubstanz im Hoden der Säugethiere. *Sitz'ber. d. Kais. Ak. d. Wissensch.*, 65 (Abt. 3): 77-100.
- (74) HUNT, H. L. 1922. Experiences in testicle transplantation. *Endocrinology*, 6: 651-654.
- (75) HUNTER, JOHN. 1880. *Observations on Certain Parts of the Animal Economy*. Philadelphia. Haswell, Barrington and Haswell, edition 1880.
- (76) JACOBSON, A. 1879. Zur pathologischen Histologie der traumatischen Hodenentzündung. *Arch. f. Path. Anat. u. Physiol.* 75: 349-397.
- (77) KASAI, K. 1908. Über die Zwischenzellen des Hodens. *Virchow's Arch. f. Path. Anat. u. Physiol.*, 194: 1-17.
- (78) KEYES, E. J., AND D. W. MACKENZIE. 1917. The operative treatment of cryptorchidism. *Jour. Amer. Med. Assoc.*, 68: 349-351.
- (79) KOSTITCH, A. 1921. Sur L'involution du processus spermatogenetique provoquée par l'alcoolisme Expérimental. *C. R. Soc. Biol.*, 84: 674-676.
- (80) KUNTZ, ALBERT. 1919. Experimental degeneration in the testis of the dog. *Anat. Record*, 17: 221-233.
- (81) ———. 1921. Degenerative changes in the seminal epithelium and associated hyperplasia of the interstitial tissue in the mammalian testis. *Endocrinology*, 5: 190-204.
- (82) KYRLE, J. 1911. Über die regenerationsvorgänge im tierischen und menschlichen Hoden. *Sitz'ber. d. Kais. Akad. Wien*. 120 (Abt. 3): 1-124.
- (83) LENKOSSEK (VON) M. 1897. Beiträge zur Kenntniss der Zwischenzellen des Hodens. *Arch. f. Anat. u. Physiol.*, pp. 65-85.
- (84) LESPINNASSE, V. D. 1913. Transplantation of the testicle. *Jour. Amer. Med. Assn.*, 61: 1869.
- (85) ———. 1924. The testicle as a gland of internal secretion. *Endocrinology and Metabolism* (Appleton, N. Y.), 2: 491-522.
- (86) LEYDIG, F. 1850. Zur Anatomie der männlichen Geschlechtsorgane und Analdrüsen der Säugethiere. *Zeitschr. f. Wissensch. Zool.*, 2: 1-37.
- (87) LICHTENSTERN, ROBERT. 1924. Die Überpflanzung der männlichen Keimdrüse. *Wien*. Julius Springer.
- (88) LILLIE, F. R. 1917. The free-martin: a study of the actions of sex hormones in the foetal life of cattle. *Jour. Exp. Zool.*, 23: 371-452.
- (89) ———. 1923. Supplementary notes on twins in cattle. *Biol. Bulletin*, 44: 47-78.
- (90) LILLIE, F. R., AND K. F. BACOM. 1922. An early stage of the free-martin and the parallel history of the interstitial cells. *Science*, 55: 624-625.
- (91) LIPSCHUTZ, A. 1919. Die Pubertätsdrüse und ihre Wirkungen. *Berne*.
- (92) ———. 1922. The so-called compensatory hypertrophy of the testicle after unilateral castration. *Jour. Physiol. (Lond.)*, 56: 451-458.
- (93) ———. 1924. The internal secretions of the sex glands. *Baltimore*, Williams & Wilkins Co.
- (94) LIPSCHUTZ, OTTOW, AND WAGNER. 1921. Du pole inférieur du testicule dans la castration partielle (and other short papers). *C. R. Soc. Biol.*, 83: 140; 85: 42, 86, 88, 638.
- (95) ———. 1922. On the hypertrophy of the interstitial cells in the testicle of the guinea pig under different experimental conditions. *Proc. Roy. Soc., B.*, 93: 132-142.
- (96) LODGE, A. 1895. Zur Transplantation der Hoden bei Hähnen. *Wien. Klinische Wochenschr.*, 8: 345.
- (97) LONG, E. R. 1924. Tuberculosis reinfection and the tuberculin reaction in the testicle of the tuberculous guinea pig. *Amer. Jour. of Tuberculosis*, 9: 215-253.
- (98) LONG, E. R., AND M. SEYFARTH. 1924. The testicle as an indicator of allergy in the hypersensitiveness of infection and anaphylaxis. *Amer. Jour. of Tuberculosis*, 9: 254-263.
- (99) LUNARSKI, O. 1896. Ueber das Vorkommen krystallinischer und krystalloider Bildungen in den Zellen des menschlichen Hodens. *Arch. f. Path. Anat. u. Physiol.*, 145: 316-335.
- (100) LYDSTON, G. F. 1916. Sex gland implantation. *Jour. Amer. Med. Assn.*, 66: 1540-1543.
- (101) ———. 1918. Cases showing remote results of testicle implantation. *Jour. Amer. Med. Assn.*, 70: 907-908.
- (102) ———. 1919. Further observations on sex gland implantation. *Jour. Amer. Med. Assn.*, 72: 396-398.

- (103) McKENNA, C. M. 1921. Testicle transplantation. Report and demonstration of a case. *Illinois Med. Jour.*, 40: 228-229.
- (104) MARSHALL, F. H. A. 1911. The male generative cycle in the hedgehog. *Jour. of Physiol. (Lond.)*, 43: 247-259.
- (105) ———. 1912. On the effects of castration and ovariectomy upon sheep. *Proc. Roy. Soc. (Lond.)*, B., 85: 27.
- (106) MARSHALL AND JOLLY. 1907. Results of removal and transplantation of ovaries. *Trans. Roy. Soc. Edinburgh*, 45.
- (107) MASON, K. E. 1925. A histological study of sterility in the albino rat due to a dietary deficiency. *Proc. Nat. Acad. Sci.*, 11: 377-382.
- (108) MATTILL, H. A., AND J. S. CARMAN. 1923. The degeneration of the testis of rats on a milk diet. *Proc. Soc. Exp. Biol. and Med.*, 20: 420.
- (109) MAXIMOW, A. 1899. Die histologischen Vorgänge bei der Heilung von Hodenverletzungen und die Regenerationsfähigkeit des Hodengewebes. *Beiträge z. Path. Anat.*, 26: 230-316.
- (110) MILLS, R. G. 1919. The pathological changes in the testes in epidemic pneumonia. *Jour. Exp. Med.*, 30: 505-519.
- (111) MONOD, C., AND G. ARTHAUD. 1887. Contribution à l'étude des alterations du testicule ectopique et de leurs conséquences (infencondite). *Arch. gen. de Med.* 7th ser. 20: 641-652.
- (112) MOORE, CARL R. 1919. On the properties of the gonads as controllers of somatic and psychical characteristics: 1. The Rat. *Jour. Exp. Zool.*, 28: 137-160.
- (113) ———. 1919. II. Growth of gonadectomized male and female rats. *Jour. Exp. Zool.*, 28: 459-467.
- (114) ———. 1920. The production of artificial hermaphrodites in mammals. *Science*, 52: 179-182.
- (115) ———. 1921. III. Artificial hermaphroditism in rats. *Jour. Exp. Zool.*, 33: 129-171.
- (116) ———. 1921. IV. Gonad transplantation in guinea pig. *Jour. Exp. Zool.*, 33: 365-389.
- (117) ———. 1922. V. The effects of gonadectomy in the guinea pig, on growth, bone length, and weight of organs of internal secretion. *Biol. Bull.*, 43: 285-312.
- (118) ———. 1922. Cryptorchidism experimentally produced. *Proc. Soc. Zool. Anat. Rec.*, 24: 383.
- (119) ———. 1923. On the relationship of the germinal epithelium to the position of the testis. *Proc. Assoc. Anat. Anat. Rec.*, 25: 142.
- (120) ———. 1924. The behavior of the germinal epithelium in testis grafts and in experimental cryptorchid testes (rat and guinea pig). *Science*, 59: 41-44.
- (121) ———. 1924. The behavior of the testis in transplantation, experimental cryptorchidism, vasectomy, scrotal insulation, and heat application. *Endocrinology*, 8: 493-508.
- (122) ———. 1924. VI. Testicular reactions in experimental cryptorchidism. *Amer. Jour. Anat.*, 34: 269-316.
- (123) ———. 1924. VIII. Heat application and testicular degeneration; the function of the scrotum. *Amer. Jour. Anat.*, 34: 337-358.
- (124) ———. 1925. Sex determination and sex differentiation in birds and mammals. *The Amer. Naturalist*, 59: 177-190.
- (125) ———. 1926. IX. Testis graft reactions in different environments (rat). *Amer. Jour. Anat.*, Vol. (in press).
- (126) MOORE, CARL R., AND H. D. CHASE. 1923. Heat application and testicular degeneration. *Proc. Soc. Zool. Anat. Rec.*, 26: 344.
- (127) MOORE, CARL R., AND WM. J. QUICK. 1923. A comparison of scrotal and peritoneal temperatures. *Proc. Soc. Zool. Anat. Rec.*, 26: 344.
- (128) ———. 1924. The scrotum as a temperature regulator for the testes. *Amer. Jour. Physiol.*, 68: 70-79.
- (129) ———. 1924. VII. Vasectomy in the rabbit. *Amer. Jour. Anat.*, 34: 317-336.
- (130) MOORE, CARL R., AND R. OSLUND. 1923. Experimental studies on sheep testes. *Proc. Soc. Zool. Anat. Rec.*, 26: 343.
- (131) ———. 1924. Experiments on the sheep testis-cryptorchidism, vasectomy and scrotal insulation. *Amer. Jour. Physiol.*, 67: 595-607.
- (132) MOORE, R. T. 1916. A case of testicle grafting with unexpected results. *Jour. Amer. Med. Assn.*, 67: 741-742.
- (133) MYERS, B. D. 1915. Histological changes in testes following vasectomy. *Proc. Soc. Anat. Anat. Record*, 20: 228.
- (134) OSLUND, ROBT. 1924. A study of vasectomy on rats and guinea pigs. *Amer. Jour. Physiol.*, 67: 422-443.
- (135) ———. 1924. Vasectomy on dogs. *Amer. Jour. Physiol.*, 70: 111-117.
- (136) ———. 1924. Interstitial cell hypertrophy. *Amer. Jour. Physiol.*, 69: 589-598.

- (137) OSLUND, ROBT. 1924. Vasectomy and rejuvenescence. *Science*, 60: 419-421.
- (138) PHILIPP, 1907. Effects of X-rays on testes in man. Quoted in Osler's *Modern Medicine*, Vol. 1, p. 61.
- (139) PLATO, J. 1897. Die interstitiellen Zellen des Hodens und ihre physiologische Bedeutung. *Arch. f. Mik. Anat.*, 48: 250-304.
- (140) ———. 1897. Zur Kenntniss der Anatomie und Physiologie des Geschlechtsorgane. *Arch. f. Mik. Anat.*, 50: 640-685.
- (141) PONCET, A. 1903. De l'influence de la castration sur le développement du squelette. *C. R. Soc. Biol.*, 55: 65-67.
- (142) RASMUSSEN, A. T. 1917. Seasonal changes in the woodchuck (*marmota monax*). *Amer. Jour. Anat.*, 22: 475-515.
- (143) ———. 1918. Cyclic changes in the interstitial cells of the ovary and testis in the woodchuck (*marmota monax*). *Endocrinology*, 2: 353-404.
- (144) REGAUD, C. 1904. État des cellules interstitielles du testicule chez la taupe pendant la période de spermatogenèse et pendant l'état de repos de canalicules séminaux. *C. R. d. l'assoc. d. Anat.* p. 54 (not seen in original).
- (145) REGAUD AND J. BLANC. 1906. Action des Rayons X sur les diverses generations de la lignée spermatique. Extrême sensibilité des spermatogonies à ces rayons (and other titles). *C. R. Soc. Biol.*, 61: 163-165, 390-392, 652-654, 731-733.
- (146) REGAUD AND G. DUBREUIL. 1907. Action des rayons de Rontgen sur le testicule de lapin. I. conservation de la puissance virile et sterilization. *C. R. Soc. Biol.*, 63: 647-649.
- (147) ———. 1908. Action des rayons de Rontgen sur le testicule des animaux impubères; immunité (relative) de l'épithélium séminale. *C. R. Soc. Biol.*, 65: 393-395.
- (148) REGAUD AND TH. NOGIER. 1909. Sterilization complete et définitive des testicules du rat, sans aucune lésion de la peau, par une application unique de rayons X filtrés. *C. R. Acad. Sci.*, 149: 1398-1401.
- (149) REGAUD AND POLICARD. 1901. Étude comparative du testicule du porc normal, impubère et ectopique, au point de vue des cellules interstitielles. *C. R. Soc. Biol.*, 53: 450-452.
- (150) REINKEN. 1896. Beiträge zur Histologie des Menschen. *Arch. f. Mik. Anat.*, 47: 34-44.
- (151) RETTERER, ED. 1919. Evolution des greffes testiculaires sur le bouc. *C. R. Soc. Biol.*, (152) RETTERER, ED. 1919. Evolution des greffes testiculaires du belier. *C. R. Soc. Biol.*, 82: 1099-1102.
- (153) RETTERER, AND S. VORONOFF. 1921. Evolution du testicule après ligature des vaisseaux testiculaires. *C. R. Soc. Biol.*, 85: 153-156.
- (154) ———. 1922. Effets locaux et généraux dus à la résection des canaux déferents. *C. R. Soc. Biol.*, 86: 1073-1075.
- (155) RIBBERT, HUGO. 1898. Über Transplantation von Ovarium, Hoden und Mamma. *Arch. f. Entw'mech.*, 78: 688-708.
- (156) RICHON, M. L., AND P. JEANDELIZ. 1903. Influence de la castration et de la résection sur le développement des organes génitaux externes chez le jeune lapin. Rôle des cellules interstitielles du testicule. Hypothèse sur la pathogenie de l'infantilisme. *C. R. Soc. de Biol.*, 55: 1685-1687.
- (157) SAND, KNUD. 1919. Experiments on the internal secretion of the sexual glands, especially on experimental hermaphroditism. *Jour. Physiol. (Lond.)*, 53: 257.
- (158) ———. 1921. Études expérimentales sur les glandes sexuelles chez les mammifères. *Jour. de Physiol.*, 19: 304-322.
- (159) ———. 1921. Expériences sur la résection du "vas deferens". *Jour. de Physiol.*, 19: 494-503.
- (160) ———. 1921. Études expérimentales sur les glandes sexuelles chez les mammifères. Cryptorchidie expérimentale. *Jour. de Physiol.*, 19: 515-527.
- (161) ———. 1921. Vasectomie pratiquée chez un chien dans un but de régénération. *C. R. Soc. Biol.*, 85: 1201.
- (162) ———. 1922. L'hermaphrodisme expérimental. *Jour. de Physiol.*, 20: 472-487.
- (163) ———. 1923. Vasoligature (epididymectomy) employed ad mod. Steinach with a view to restitution in cases of senium and other states (impotency, depression). *Acta Chirurgica Scandinavica*, 55: (suppl. 4) 387-426.
- (164) ———. 1923. Experiments on the endocrinology of the sexual glands. *Endocrinology*, 7: 273-301.
- (165) SCHULTZ. 1900. Transplantation der Ovarien auf männliche thiere. *Centr'bl. f. all. path.*, 2: 200.
- (166) SCHMIDT, PETER. 1914. The Theory and Practice of the Steinach Operation. London. Wm. Heinemann.
- (167) SELLHEIM. 1899 (abstract). Jahresbericht der Anat., 5: 1., p. 191, II., p. 221.

- reaction in the testicle as an indicator of the hypersensitiveness of infection. *Jour. Infectious Diseases*, 35: 489-497.
- (169) SHATTOCK, S. G., AND C. G. SELIGMANN. 1904. Observations upon the acquirement of secondary sexual characters, indicating the formation of an internal secretion by the testicle. *Proc. Roy. Soc. Lond.*, 73: 49 and 1905-*Trans. Path. soc. Lond.*, 56: 57-80.
- (170) SIMMONDS. 1898. Ueber die Ursachen der Azoospermie. *Berl. Klin. Wochenschr.*, 35: 806.
- (171) ———. 1913. Ueber Mesothoriumschädigung des Hodens. *Deut. Med. Wochenschr.*, 39: 2291-2292.
- (172) ———. 1921. Ueber das Verhalten des menschlichen Hodens bei narbigen Samenleiterverschluss. *Deut. Med. Wochenschr.*, 47: 665.
- (173) SPENCER, HERBERT. 1899. *The Principles of Biology*. Appleton. New York.
- (174) STANLEY, L. L. 1921. Testicular substance implantation. *Endocrinology*, 5: 708-714.
- (175) ———. 1922. An analysis of one thousand testicular substance implantations. *Endocrinology*, 6: 787-794.
- (176) STANLEY AND G. D. KELKER. 1920. Testicle transplantation. *Jour. Amer. Med. Assn.* 75: 1501-1503.
- (177) STEINACH, E. 1910. Geschlechtstrieb und echt sekundäre Geschlechtsmerkmale als Folge der innersekretorischen Funktion der Keimdrüsen. *Centr'bl. f. Physiol.*, 24: 551-566.
- (178) ———. 1911. Umstimmung des Geschlechtscharakters bei Säugetieren durch Austausch der Pubertätsdrüsen. *Centr'bl. f. Physiol.*, 25: 723-725.
- (179) ———. 1912. Willkürliche Umwandlung von Säugetiereimännchen in Tiere mit ausgeprägt weiblichen Geschlechtscharakteren und weiblicher Psyche. *Pflügers Archiv*, 144: 71-106.
- (180) ———. 1913. Feminisierung von Männchen und Maskulierung von Weibchen. *Centr'bl. f. Physiol.*, 27: 717-723.
- (181) ———. 1916. Pubertätsdrüsen und Zwitterbildung. *Arch. f. Entw'mech.*, 42: 307-330.
- (182) ———. 1920. Künstliche und natürliche Zwitterdrüsen und ihre analogen Wirkungen. *Arch. f. Entw'mech.*, 46: 12-28.
- (183) ———. 1920. Verjüngung durch experimentells Neubelebung der alternden Pubertätsdrüse. *Arch. f. Entw'mech.*, 46: 557-618.
- (184) STEINACH AND HOLZNECHT. 1916. Erhöhte Wirkungen der inner Sekretion bei Hypertrophie der Pubertätsdrüsen. *Arch. f. Entw'mech.*, 42: 490-505.
- (185) STIEDA, L. 1897. Die Leydig'schen Zwischensubstanz des Hodens. *Arch. f. Mik. Anat.*, 48: 692-695.
- (186) TANDLER, J., AND S. GROSZ. 1907. Ueber den Einfluss der Kastration auf den Organismus. *Wien. Klin. Wochenschr.*, 20: 1596.
- (187) ———. 1908. Untersuchungen an Skopzen. *Wien. Klin. Wochenschr.*, 21: 277-282.
- (188) ———. 1910. Über den Einfluss der Kastration auf den Organismus. *Arch. f. Entw'mech.*, 30: 236-253.
- (189) ———. 1911. Über den Saisondimorphismus des Maulwurfs Hodens. *Arch. f. Entw'mech.*, 33: 297-302.
- (190) TIEDJE, H. 1921. Unterbindungsbefunde am Hoden unter Berücksichtigung der Pubertätsdrüsenfrage. *Deut. Med. Wochenschr.*, 47: 352-354.
- (191) THORKE, M. 1922. The present position of testicle transplantation in surgical practice; a preliminary report of a new method. *Endocrinology*, 6: 771-775.
- (192) ———. 1924. *The human testis and its diseases*. Lippincott. Philadelphia.
- (193) VAN WAGENEN, G. 1924. Degeneration of the germinal epithelium in the testis of the rat as a result of efferent duct ligation. *Proc. Soc. Anat. Anat. Record*, 27: 189.
- (194) ———. 1925. Changes in the testis of the rat following ligation of the ductuli efferenti. *Proc. Soc. Anat. Anat. Record*, 29: 399.
- (195) VILLEMEN, F. 1906. Sur la regeneration de la glande seminale après destruction par les rayons X. *C. R. Soc. Biol.*, 60: 1076-1077.
- (196) VORONOFF, S. 1923. *Greffes Testiculaires*. Paris. Doin.
- (197) WAGNER, KARL. 1925. Sind die Zwischenzellen des Säugetierhodens Drüsenzellen? *Biologia Generalis*, 1: 22-31.
- (198) WALLACE, C. S. 1905. The results of castration and vasectomy upon the prostate gland in the enlarged and normal condition. *Trans. Path. Soc. (Lond.)*, 56: 80-106.
- (199) WAKELIN BARRATT, J. O. AND G. ARNOLD. 1911. Cell changes in the testis due to X-rays. *Arch. f. Zellforschung*, 7: 242-276.
- (200) WEICHSSELBAUM A., AND J. KYRLE. 1912. Über die Veränderung der Hoden bei chronischem Alkoholismus. *Sitz'ber. d. Kais. Akad. Wien*, 121: 51-70.

- (201) WHEELON, C. H. 1921. Observations on two testes nine months following vasectomy. *Endocrinology*, 5: 307-308.
- (202) WHITFIELD, R. H. 1904. The embryonic development of the interstitial cells of Leydig. *Amer. Jour. Anat.*, 3: 167-182.
- (203) ——. 1904. Studies of the interstitial cells of Leydig. 2. Their post embryonic development. *Amer. Jour. Anat.*, 4: 193-197.
- (204) ——. 1908. Studies of the interstitial cells of Leydig. 3. Histology. *Anat. Record*, 1: 213-227.
- (205) ——. 1908. A peculiar case of cryptorchidism and its bearing upon the problem of the function of the interstitial cells of the testis. *Anat. Record*, 2: 177.
- (206) ——. 1909. The interstitial cells of an hermaphrodite horse. *Anat., Record*, 3: 264.
- (207) ——. 1912. On the chemical nature of certain granules in the interstitial cells of the testis. *Amer. Jour. Anat.*, 14: 63-71.
- (208) ——. 1913. The structure of a testis from a case of human hermaphroditism. *Anat. Record*, 7: 83-90.
- (209) WIEDERSHEIM. 1907. *Comparative Anatomy of Vertebrates*. The Macmillan Company. New York.
- (210) WILLIAMS, B. H. 1921. The structure and homologies of the free-martin gonads. *Jour. Exp. Zool.*, 33: 63-127.
- (211) WOLBACH, S. B. 1919. Comments on the pathology of fatal influenza cases, as observed at Camp Devens, Mass. *Johns Hopkins Hospital Bull.*, 30: 104-105.
- (212) WOOLLAND, W. 1903. On the phylogenetic cause of the transposition of the testes in mammals; with remarks on the evolution of the diaphragm and the metamorphic kidney. *Proc. Zool. Soc. Lond.*, 1903, part 1: 319-340.





SYMBIOSIS AMONG ANIMALS WITH SPECIAL REFERENCE TO TERMITES AND THEIR INTESTINAL FLAGELLATES

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I. INTRODUCTION

Origin and meaning of term symbiosis

THE term symbiosis as originally used by De Bary (1879) means the living-together of two organisms on a partnership basis. The partnership may be between animal and plant, animal and animal, plant and plant. Such associations vary vastly in degree, but each organism must receive some benefit from its partner or else the association is not one of symbiosis. It is also usually true that one partner is much smaller than the other, the small one being the symbiote or parasite and the large one the host, which, strictly speaking, is also a symbiote or partner. Host and parasite are parasitological terms for the symbiotes or partners. Meyer (1925) has recently pointed out that the term symbiont is a misnomer; the Greek word for "companion" or "partner" is symbiote.

How symbiosis is studied

It is a most difficult matter, indeed, to tell where symbiotic associations end and others begin. The only crucial method available in most cases at present is to first break the association, study each partner separately, determine what it can and cannot do when alone, then reestablish the partnership and study the reunited partners. Such a procedure is

infinitely more difficult than to reason how one partner, particularly the microscopic one, might easily help the other; consequently very few definitely established examples of symbiosis are known. Most of our information consists of possibilities.

Some examples of symbiosis

The intracellular and intestinal yeast-like and bacteria-like bodies present in all individuals of many groups of insects, and transmitted in most cases from generation to generation through the egg, may or may not be symbiotes—nobody knows. The literature on the presence, character, and possible symbiotic rôle that these microorganisms play in the lives of their insect hosts is immense (Portier, 1918; Buchner, 1921; Uichanco, 1924; Meyer, 1925; give extensive references), and it is unnecessary to add to it by giving a discussion here. What needs to be done is to devise some method or combination of methods by which these microorganisms may all be taken from their hosts without injury—a difficult undertaking. Here is a most fruitful field of investigation awaiting an opening. Who will open it?

The intracellular bacteria of certain mollusks have been termed symbiotes, although Meyer (1925), who has recently made a detailed investigation of some of these microorganisms in relation to their molluskan hosts, says the word symbiote

"is used more for the sake of convenience than as the result of an absolute conviction that the phenomenon is one of true symbiosis." He continues, "from the experiments and findings reported it is easy to assume that the mollusks derive some benefit from the intracellular bacteria as anabolists or catabolists of metabolic waste products, but, what possible benefit can the microorganisms derive from the association?"

Green (*Zoochlorella*) and yellow (*Zooxanthella*) algae are closely associated with many animals: Turbellarians, Mollusks, Annelids, Bryozoans, Coelenterates, Rotifers, and Protozoa. In some of these animal-plant associations it has been claimed by a number of investigators that the gas liberated contains much more than the normal percentage of oxygen, in some associations as high as 55 per cent; whereas the colorless varieties of these animals, that is those without algae, give off a very much smaller percentage of oxygen, if any at all. Such associations are regarded as helpful or beneficial to both partners. The algae supply the animal with oxygen for which they get carbon dioxide and nitrogen in return. Perhaps a fair number of these associations are beneficial to both partners, but certainly very few of them are absolutely necessary for the existence of the partners concerned. In one of the Turbellaria, *Convoluta roscoffensis*, the larvae, according to Keeble and Gamble, are colorless, that is, do not harbor algae, at the time of hatching and can only feed themselves for a week, by which time they have gotten algae. For a while, then, they live on the products given off by the algae, but later, after having reached a more advanced stage in their life-cycle, they become capable of digesting the algae, and the symbiosis—at least for the algae digested—ends and the association merges

Minute bacteria-like luminescent bodies associated with fishes, tunicates, cephalopods, and insects have been studied by a number of investigators, and it is practically certain that at least some of these associations are symbiotic in character, that is to say, each of the organisms is benefited in some way, however slight the benefit may be.

Relation of symbiosis to other forms of parasitism

One of the most interesting things about symbiosis is its origin and relation to other host-parasite associations: commensalism, that association in which hosts tolerate their parasites as guests or messmates; and true parasitism, that association in which the parasites live altogether or in part at the expense of their hosts. In a commensalistic association neither party is benefited nor injured. Obviously, associations with such an equilibrium must be extremely rare, for many of the so-called commensalistic parasites cannot live outside of their hosts and, of course, must be benefited. In true parasitism either the host or the parasite is injured: when a host develops immunity and frees itself of parasites, the parasites are injured; until this occurs the host receives the principal injury. Parasitism proper, or in the general sense, according to fairly well-established usage, covers all three associations: commensalism, symbiosis, and true parasitism. It would be much better, however, to use the term symbiosis, which means living together, and under it include commensalism, mutualism, and parasitism. However desirable such a change in terminology may be, it is not an easy matter to make it, and I shall not attempt it at this time.

Symbiosis occupies perhaps somewhat of a mid-way position between commensalism and true parasitism, and, from our meagre information concerning its possible

origin, is probably derived from them—just how, we do not know. Ideal partnership or symbiosis, that condition in which each party concerned gives as much as it receives, is rarely, if ever, realized; the partnership is usually one-sided, that is, one partner does most of the giving. Such associations from the standpoint of the partner that does most of the giving, are near true parasitism; from the standpoint of the partner that does most of the receiving, they are near commensalism.

II. GENERAL CONSIDERATIONS OF TERMITES AND THEIR PROTOZOA

Species and families harboring protozoa

Approximately 1500 species of termites have been described and have been grouped in four families: Mastotermitidae, Kalotermitidae, Rhinotermitidae, and Termitidae. All species that have been examined from the first three families (Cleveland, 1923) have been found to harbor a teeming menagerie of intestinal protozoa—the protozoa in these insects weigh almost as much as the insects themselves. Most species of the Termitidae that have been examined have not been found to harbor any protozoa at all, and in those where they have been found the quantity can in no way be compared to that of the other families. Dr. Harold Kirby has recently collected and shipped me a large number of termites from Panama and Costa Rica. Small amoebae and flagellates are present, but not abundant, in two species of *Amisotermes*, *A. beaumonti* Banks and *H. medius* Banks. Larger, more abundant and wood-ingesting amoebae are present in *Mirotermes panamaensis* Snyder. Small tetramitid flagellates are present in *Orbognathotermes wheeleri* Snyder. Most of the Termitidae examined had no protozoa. A list of the Termitidae examined and a description of the protozoa found, will be published by Dr. Kirby soon.

More investigation may determine whether or not the Termitidae are losing their protozoa or are just beginning to harbor them. The situation is a most interesting one, indeed, and certainly should be investigated thoroughly. Are we observing in this family of termites the beginning or the last stage in the closing of a symbiotic association?

Partnerships with fungi

It has been shown by Dörflein (1905), Petch (1906), Fuller (1920, 1921) and others that some of the Termitidae with no protozoa in them have formed partnerships with fungi by giving over a certain portion of their nest (the fungus garden) to the growth and cultivation of the fungus which they eat along with soil, cellulose, and hemicellulose which the fungus has acted upon. Fuller (1921) has observed the deliberate removal of certain parts of the fungus garden during prolonged droughts followed by a week or so of rain to propitious places outside the nest.

Food

The Termitidae as a rule do not feed solely on wood or cellulose material, and when they do eat wood, it is usually very much more decayed than that which the protozoa-harboring families eat. The Kalotermitidae feed on wood that has begun to decay very little if at all—several species feed on hard, dry wood that has not begun to decay in the least. Two genera of the Rhinotermitidae (*Reticulitermes* and *Termopsis*) have lived for more than two years on a diet of pure cellulose (Cleveland, 1925a). A number of efforts have been made recently to get Termitidae to live on a cellulose (filter paper) diet. *Obtusitermes*, *Anoplotermes*, *Orbognathotermes*, *Mirotermes*, and *Amisotermes* in large numbers have been given a cellulose diet

under various conditions as near natural as was possible in the laboratory. Some of them ate the cellulose, but others did not, and none of them were able to live longer than a month. They usually died much sooner. However, it is a difficult matter to keep most Termitidae in confinement, and for this reason it should not be stated yet that these termites are unable to live on a cellulose diet. It is only after considerable experience, in fact, that one is able to keep any termite perfectly normal under laboratory confinement. If these termites are able to live on a cellulose diet, it is highly probable that they are assisted in some way by microorganisms. It is not likely that they digest cellulose themselves, although we do not know of any symbiotes that do it for them. Many of them are filled with a wriggling horde of large spirochaetes, which may be easily removed and without injury to their host by confining the termites in oxygen under pressure for about the same time that it takes to remove or kill termite protozoa. Some of them have intestinal fungi, but we do not know what rôle these fungi and spirochaetes play in their host's metabolism. This should be determined.

Termite protozoa

The protozoa of termites are most interesting creatures indeed. Everyone who has observed them has marvelled at their abundance, interesting structures, peculiar adaptation and mode of living, and has wondered how on earth so many of them live in a single termite and what they do, that is, how they live and what relation they have to the termites in which they live, move, and have their being.

It has been stated by a number of investigators that protozoa are present only in the workers and soldiers. This is not true. They are present in all wood-eating

and wood-feeding members of a colony. In those termites where a worker caste is present, the old and enlarged reproductive adults do not feed on wood—the workers feed them, and when they do, the protozoa disappear. When no worker caste is present, the wood-feeding habit is never given up, the protozoa are never lost, and no greatly enlarged adults are found.

As a rule protozoa—living or dead—are not present in the fecal pellets of termites. They do not pass out with fecal material in the way that the intestinal protozoa of other animals usually do. They are perhaps used as food for their host. Young termites, however, seem to get protozoa, in some unknown manner, from the ani of the older members of the colony. Some special provision seems to be made to give them to the young, perhaps by giving off extra and more liquid material than pellets, from the anus. It is remarkable how soon the larvae get protozoa in their guts. Out of twenty-five larvae of *Termopsis* experimented with, fifteen acquired protozoa within twenty-four hours from the time of hatching. Larvae kept by themselves from the time of hatching never get protozoa and they die in a week or thereabouts.

The plates at the end of this paper show several genera of termite protozoa selected at random from more than forty that are known. Evidently only a beginning has been made in the study of these protozoa; one can find new genera and species in almost any termite. Seven or eight genera sometimes occur in a single termite host; in fact it is most unusual to find less than four genera, except in the Termitidae. It is quite probable that when all the termite-inhabiting protozoa are known, representatives of practically all parasitic or entozoic protozoa of other animals will be found in termites. Does this mean that the evolution of parasitic protozoa has

been going on longer in termites than in other animals, or does it mean that protozoa have found a much more favorable environment in termites than in other animals? Does a symbiotic association, which should give the most favorable environment for a protozoon, encourage evolution? Do more changes occur, or are more of those that do occur preserved? We do not know. What little information we have regarding the geographical distribution of termites and their intestinal protozoa indicates that there has been a parallel evolution of the two groups of organisms, which, if true, means that the symbiosis has perhaps been established for a very long time. It is also probably true that many pathogenic protozoa have become extinct by eliminating their hosts, while symbiotic protozoa have made it possible for many variations in their hosts to survive and for their hosts to become very numerous; and if commensalistic protozoa were once pathogenic, there has perhaps been a great loss of species and genera in their evolution—only the less pathogenic ones survived and gradually became commensals.

III. METHODS AND RESULTS OF FREEING TERMITES OF THEIR PROTOZOA

Incubation

A fairly convenient method of freeing termites of their protozoa is to incubate them at 36°C. for twenty-four hours (Cleveland, 1924). Such a treatment perhaps injures some of them but not a great deal when the proper moisture concentration is maintained. This perhaps can best be done by confining the termites with wood in a vaseline-sealed chamber with a very small amount of moist cotton. With no moisture, the termites become too dry and are injured; with a great deal of moisture, molds grow rapidly and injure them.

When the common eastern termite, *Reticulitermes flavipes* Kollar, is incubated as described above, all of its intestinal protozoa are removed within twenty-four hours; all protozoa in most individuals are killed in twenty hours. The differential death points of termites and their protozoa when incubated or heated for ten minutes are great enough to allow the removal of the protozoa without killing the termites, but such a method has not proven as useful, so far, as one with a longer heating period.

Experiments have been carried out recently on the incubation of many species of termites from Panama and Costa Rica, the details of which, when completed, will appear in another paper. It is sufficient to state here that all termite protozoa are not killed in the same time at a given temperature, that is, the time-temperature relation is not constant. It is not constant even for all the protozoa of certain termites; in *Kalotermes rabogae* at approximately 35.5°C. the trichonymphids are all killed in two days (many are killed much sooner), while it is five or six days before the calonymphids are affected at all and eight to ten days before they are all killed. At 36.5°C. the trichonymphids of this termite are killed in less than twenty-four hours, while the calonymphids are not killed in three days. But *Calcaritermes*, for instance, loses its protozoa within less than twenty-four hours when incubated at 35.5°C.

After *Reticulitermes* had been freed of its intestinal protozoa (Cleveland, 1924), it was carefully studied. As a rule it died within three weeks or thereabouts after its protozoa were taken from it. It was discovered, however, that the actual length of time required for death to take place depended on the food eaten; the more decayed the food (wood) the longer it lived. When given humus or fungus-

digested cellulose (paper), it lived very much longer and would perhaps have lived indefinitely had it been properly cared for; molds, as mentioned before, kill termites when the moisture content is high and they cannot live without a certain amount of moisture. It is difficult to maintain the right amount. The best way devised so far is to keep the termites in a closed jar or flask which is connected with a moist chamber of some sort—another flask will do—by means of a small glass tube. Once the proper amount of moisture is ascertained, it may be kept indefinitely without any attention whatever. Incidentally, this same method is very useful in keeping untreated termites under close observation in the laboratory. The moisture required by different termites differs greatly; some species of *Cryptotermes* require almost no moisture at all and can live in furniture for a long time.

The fact that the incubated termites lived very much longer, if not indefinitely, on a predigested diet of humus or fungus-digested cellulose than on their normal diet of partially decayed wood indicated that the incubation in itself was not responsible for their death. Obviously, the best way to determine whether the incubation killed the termites directly or indirectly was to incubate a large number of individuals, thus freeing them of protozoa, then replace the protozoa in one portion but not in the other, then feed each portion on the same normal diet of wood under identical conditions. This was done, and all those termites in which the protozoa were restored were able to live indefinitely, while the others all died in approximately three weeks. It was thus shown that the death of the incubated termites was due to the removal or killing off of the protozoa rather than to the incubation in itself. Here, then, is an ideal case of symbiosis; neither partner (nor symbiote)

can live without the other. A termite chews and swallows wood which the countless millions of protozoa living in it eat and digest for themselves and for the termite that maintains them in a gastronomical paradise—its gut.

Starvation

When termites are starved, practically all their large protozoa and many of their small ones die long before they do. The large protozoa in practically every species of termite die more quickly than the small ones. Perhaps the best way to carry out a starvation experiment is to place the termites in clean, flat-bottomed, dry glass vessels, and keep these in moist chambers. Here again the amount of moisture present is important. If there is too much or too little, the termites will not die of starvation.

More extensive observations and experiments have been carried out on the starvation of the large Pacific Coast termite, *Termopsis*, than on any other (Cleveland, 1925b). This termite contains protozoa of four genera (figs. 1-4) in fairly definite proportions and when starved, its largest protozoon, *Trichonympha campanula* (fig. 1), dies first. After about six days' starvation this protozoon disappears entirely. If the starvation is continued, the next largest protozoon, *Leidyopsis sphaerica* (fig. 2), disappears by the end of eight days. After twelve to fifteen days' starvation, the other protozoa, *Trichomonas termopsidis* (fig. 3) and *Streblomastix strix* (fig. 4), are greatly reduced in number, but it is impossible to remove everyone of them before the termites die or are greatly injured. Very few of them live more than twenty-five days.

If, after six days' starvation, which removes *Trichonympha*, the termites are returned to their normal wood diet, they are able to live indefinitely as shown in

table 1. *Leidyopsis*, then, which in untreated termites is seldom if ever present in such great numbers as *Trichonympha*, multiplies rapidly and takes the place of *Trichonympha* in number and, as we shall see later, as the principal symbiote. When both *Trichonympha* and *Leidyopsis* are removed by eight days' starvation, these termites, when returned to their normal diet, are able to live sixty to seventy days; whereas when all protozoa are removed (see table 1), termites live

Oxygenation

When termites are placed in oxygen under pressure, they lose their protozoa very quickly, indeed (Cleveland, 1925b, 1925c), and without being injured in the least. This is a better method of freeing them of protozoa than incubation or starvation. But here, as in incubation and starvation, all termite protozoa are not affected in the same way when oxygenated. Some of them lose their pro-

TABLE 1.

Results of various methods which have been employed in removing one or more genera of protozoa from the large Pacific Coast termite, *Termopsis nevadensis* Hagen

Every host in nature always harbors each genus. — = absent, i.e., treatment killed all protozoa of this genus and + = present, i.e., treatment had no effect.

METHODS OF TREATMENT	THE PROTOZOA				RESULT OF TREATMENT ON HOST WHEN FED ITS NORMAL WOOD DIET
	<i>Trichonympha</i>	<i>Leidyopsis</i>	<i>Trichomonas</i>	<i>Streblomastix</i>	
1. Starvation for 6 days.....	—	+	+	+	Lives indefinitely
2. Starvation for 8 days.....	—	—	+	+	Lives about 10 weeks
3. Oxygenation for 24 hours at 1 atm.....	+	+	—	+	Lives indefinitely
4. Oxygenation for 24 hours at 1 atm. Starvation for 6 days.....	—	+	—	+	Lives indefinitely
5. Oxygenation for 24 hours at 1 atm. Starvation for 8 days.....	—	—	—	+	Lives 3-4 weeks
6. Oxygenation for 7 hours at 1.5 atms.....	+	+	—	—	Lives indefinitely
7. Oxygenation for 7 hours at 1.5 atms. Starvation for 6 days.....	—	+	—	—	Lives indefinitely
8-13. Oxygenation, 1 atm., 72 hrs.; 1.5 atm., 9 hrs.; 2.5 atm., 2 hrs.; 3 atm., 1 hr. and 5 min.; 3.5 atm., 40 min.....	—	—	—	—	Lives 3-4 weeks.

only three to four weeks. Evidently, then, the remaining protozoa, *Trichomonas* and *Streblomastix*, are of some value to their hosts but are not able to keep them alive indefinitely. The removal of *Trichonympha* and *Leidyopsis* destroys the symbiotic association, although not completely, and results, finally, in the death of *Termopsis* and its protozoa. This termite has certainly formed a most intimate partnership with two of its protozoa.

tozoa when confined in an atmosphere of practically pure oxygen, that is when they are changed from an atmosphere of air with approximately 20 per cent oxygen to an atmosphere of 95 to 98 per cent oxygen; while others do not lose their protozoa until they are placed in slightly more than one atmosphere of oxygen (table 2). As the oxygen pressure increases, the time required to kill the protozoa decreases rapidly until a pressure of three and a half to four atmospheres is

reached. At a pressure of fifteen atmospheres, for instance, the protozoa are killed in about half the time that they are killed when oxygenated at a pressure of three and a half atmospheres; whereas three and a half atmospheres kills them in half the time that three atmospheres does. In other words, one-half of an atmosphere between three and three and a half atmospheres cuts down the time required to kill the protozoa as much as ten or eleven atmospheres do after three and a half to four atmospheres have been reached. Obviously, then, the best oxygenation pressure to use in breaking the

TABLE 2.

Time required at various pressures of oxygen to kill all intestinal protozoa of certain termites

PRESSURE IN ATMOSPHERES	RHINOTERMITIDAE				KALOTERMITIDAE			
	Leucotermes		Reticulitermes		Termopsis		Cryptotermes	
	Hours	Minutes	Hours	Minutes	Hours	Minutes	Hours	Minutes
1.0	24		*		72		*	
1.5	4	30	9		9		7	30
2.0	1	35	4		5		4	30
2.5	1	15	1	40	2		1	55
3.0		50		50	1	5	1	
3.5		30		30		40		35

* Not killed in ten days.

symbiosis between termites and their protozoa is somewhere between three and four atmospheres.

Work is now in progress on the relation of the protozoa of many species of termites from Panama and Costa Rica to their hosts. The work is not complete, but it is evident that some of these termites are able to live longer than three to four weeks after their protozoa have been taken from them. Many of them, however, are not. We cannot be sure that protozoa-harboring termites will die when their protozoa are killed, until actual experiment has shown that they do. Some of them, although we are inclined to doubt it, may be able to live—poorly of

Oxygenation and starvation

After having noted that oxygenation removes some termite protozoa and not others, that is, brings about a partial rather than a total defaunation, and that starvation does the same thing, it was evident that by a combination of the two partial defaunation methods interesting results might be obtained as to just what protozoa were and were not symbiotes.

The large Pacific Coast termite, *Termopsis*, as we have already seen, contains four genera of protozoa, and when oxygenated at one atmosphere, it loses *Trichomonas* (fig. 3) within twenty-four hours, but does not lose its other protozoa until three days (Cleveland, 1925b). By oxygenating this termite at a pressure of 1.5 atmospheres for seven hours it was possible to remove both *Trichomonas* and *Streblomastix* (fig. 4) from many, though never all, hosts without seriously injuring *Trichonympha* (fig. 1) and *Leidyopsis* (fig. 2). We have already noted that if this termite is starved for six days it loses *Trichonympha*, and if starved eight days it loses *Trichonympha* and *Leidyopsis*. The various protozoal combinations which may be obtained by starving and oxygenating *Termopsis* are given in table 1. Termites of each of the seven groups, and of the group with no protozoa, were fed their normal diet of wood and kept under identical conditions. Table 1 shows what happened to each group.

Either *Trichonympha* or *Leidyopsis* is able to keep its host alive indefinitely. *Trichomonas* is able to keep its host alive for a while, but not indefinitely. *Streblomastix* is of no value to its host and is not a symbiote. It may be supported either by the termites or by its protozoan neighbors, or by both. Similar work on the protozoa of other termites will perhaps show that not all termite protozoa are

LITERATURE LIST

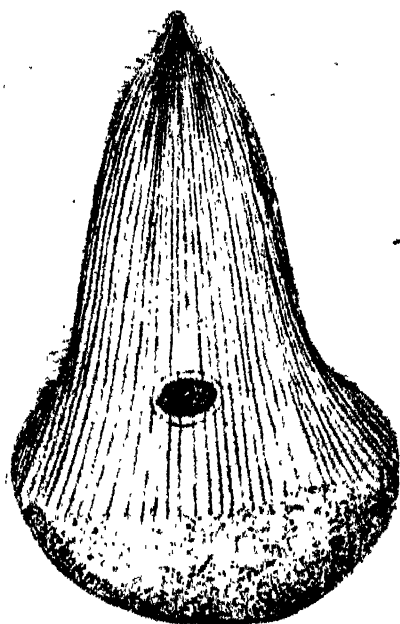
- BUCHNER, P. 1921. Tier und Pflanze in intrazellulärer Symbiose. 462 p. Berlin: Gebrüder Borntraeger.
- CLEVELAND, L. R. 1923. Correlation between the food and morphology of termites and the presence of intestinal protozoa. *Amer. Journ. Hyg.*, 3: 444-461.
- CLEVELAND, L. R. 1924. The physiological and symbiotic relationships between the intestinal protozoa of termites and their host, with special reference to *Reticulitermes flavipes* Kollar. *Biol. Bull.*, 46: 177-225.
- CLEVELAND, L. R. 1925a. The ability of termites to live perhaps indefinitely on a diet of pure cellulose. *Biol. Bull.*, 48: 289-293.
- CLEVELAND, L. R. 1925b. The effects of oxygenation and starvation on the symbiosis between the termite, *Termopsis*, and its intestinal flagellates. *Biol. Bull.*, 48: 309-327.
- CLEVELAND, L. R. 1925c. The toxicity of oxygen for protozoa in vivo and vitro: animals defaunated without injury. *Biol. Bull.*, 48: 455-468.
- DE BARY, ANT. 1879. Die Erscheinung der Symbiose. DORLEIN, F. 1906. Die Pilzkulturen der Termiten. *Verhandl. d. Deutsch. Zool. Ges.*, 15: 140-149.
- FULLER, C. 1920. *Annals Natal Museum*, 4: 235-295.
- FULLER, C. 1921. The fungus food of certain termites. *S. Afr. Journ. Nat. Hist.*, 3: 139-144.
- MEYER, K. F. 1925. The "bacterial symbiosis" in the concretion deposits of certain operculate land mollusks of the families cyclostomatidae and annulariidae. *Journ. Infect. Diseases*, 36: 1-107.
- NUTTALL, G. H. F. 1923. Symbiosis in animals and plants. Address British Association Liverpool in 1923.
- PETCH, T. 1906. The fungi of certain termite nests. *Ann. Roy. Botan. Garden Peradenya*, 3: 185-270.
- PORTIER, P. 1918. *Les Symbiotes*. 315 p. Paris: Masson et Cie.
- UICHANCO, L. B. 1924. Studies on the embryogeny and postnatal development of the aphidae with special reference to this history of the "symbiotic organ" or "mycetom." *Philippine Journ. of Sci.*, 24, 143-247.



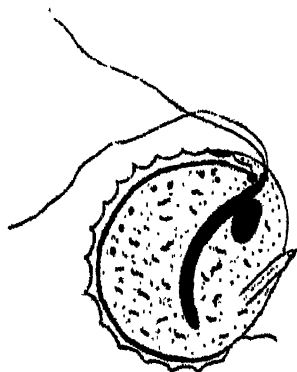
DESCRIPTION OF PLATES 1-4

FIGURES	PROTOZOON	TERMITE FOUND IN	LOCALITY
1	<i>Trichonympha campanula</i>	<i>Termopsis angusticollis</i>	Pacific Coast, U. S. A.
2	<i>Laidyopsis sphaerica</i>	<i>Termopsis angusticollis</i>	Pacific Coast, U. S. A.
3	<i>Trichomonas termopsidis</i>	<i>Termopsis angusticollis</i>	Pacific Coast, U. S. A.
4	<i>Sireblomastix strix</i>	<i>Termopsis angusticollis</i>	Pacific Coast, U. S. A.
5	<i>Microjoenia hexamitoides</i>	<i>Reticulitermes lucifugus</i>	Italy
6	<i>Districhomonas termitis</i>	<i>Archotermopsis wroughtoni</i>	India
7	<i>Holomastigotoides hemigymnum</i>	<i>Coptotermes lacteus</i>	Australia
8	<i>Macrotrichomonas pulchra</i>	<i>Glyptotermes parvulus</i>	Chile
9	<i>Devescovina glabra</i>	<i>Cryptotermes havilandi</i>	Chile
10	<i>Joemopsis cephalotricha</i>	<i>Archotermopsis wroughtoni</i>	India
11	<i>Pseudotrypanosoma giganteum</i>	<i>Porotermes adamsoni</i>	Australia
12	<i>Spirotrichonymphella pudibunda</i>	<i>Porotermes adamsoni</i>	Australia
13	<i>Holomastigotes elongatum</i>	<i>Reticulitermes lucifugus</i>	Italy
14	<i>Microspironympha porteri</i>	<i>Reticulitermes flaviceps</i>	Japan
15	<i>Pseudotrichonympha bertwigi</i>	<i>Coptotermes sjöstedti</i>	French Guinea
16	<i>Dinenympha rugosa</i>	<i>Reticulitermes speratus</i>	Formosa
17	<i>Stephanonympha sylvestri</i>	<i>Kaloterms grassii</i>	Chile
18	<i>Spirotrichonympha elongata</i>	<i>Schedorbinotermes intermedius</i>	Australia
19	<i>Diplenympha foai</i>	<i>Glyptotermes parvulus</i>	Gold Coast
20	<i>Pyronympha grandis</i>	<i>Reticulitermes speratus</i>	Formosa
21	<i>Teratonympha mirabilis</i>	<i>Reticulitermes flaviceps</i>	Formosa
22	<i>Sasurojoenina mirabilis</i>	<i>Epicalotermes aethiopicus</i>	Eritrea
23	<i>Joenia pulchella</i>	<i>Porotermes adamsoni</i>	Australia

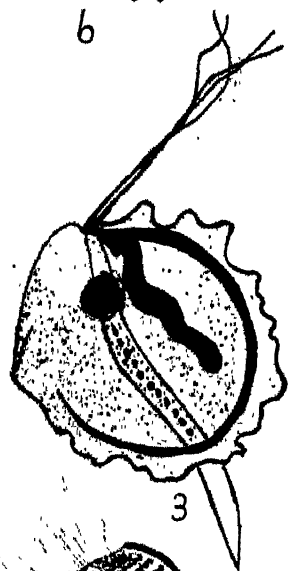
Figures 1, 2, 4 after Kofoid and Swezy; 5, 7, 8, 9, 10, 11, 12, 15, 17, 18, 19, 22, 23 after Grassi; 6, 10 after Cutler; 13, 14, 16, 20, 21 after Koidzumi.



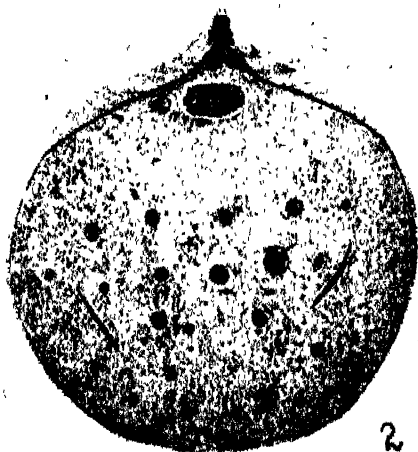
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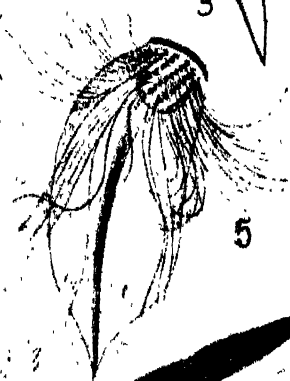
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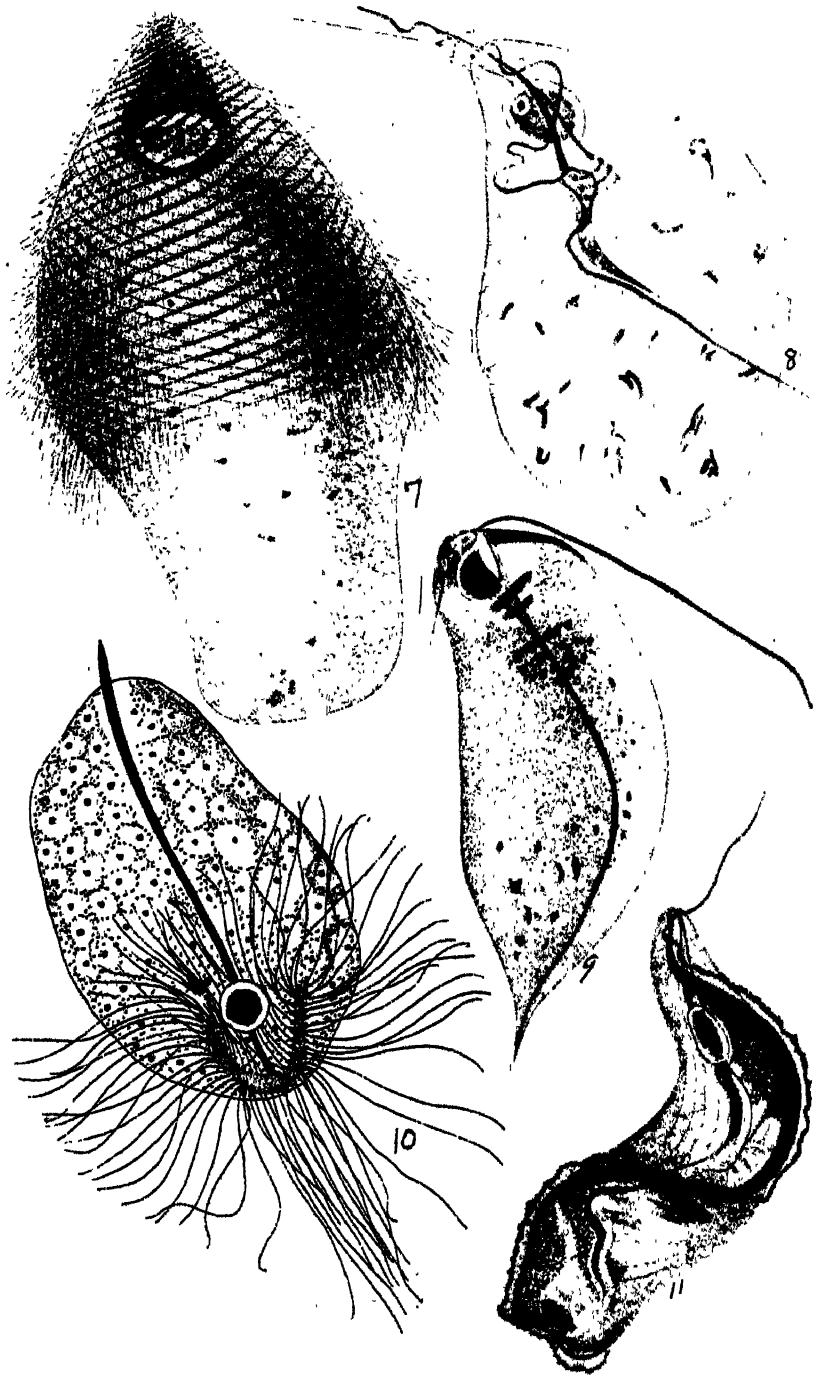
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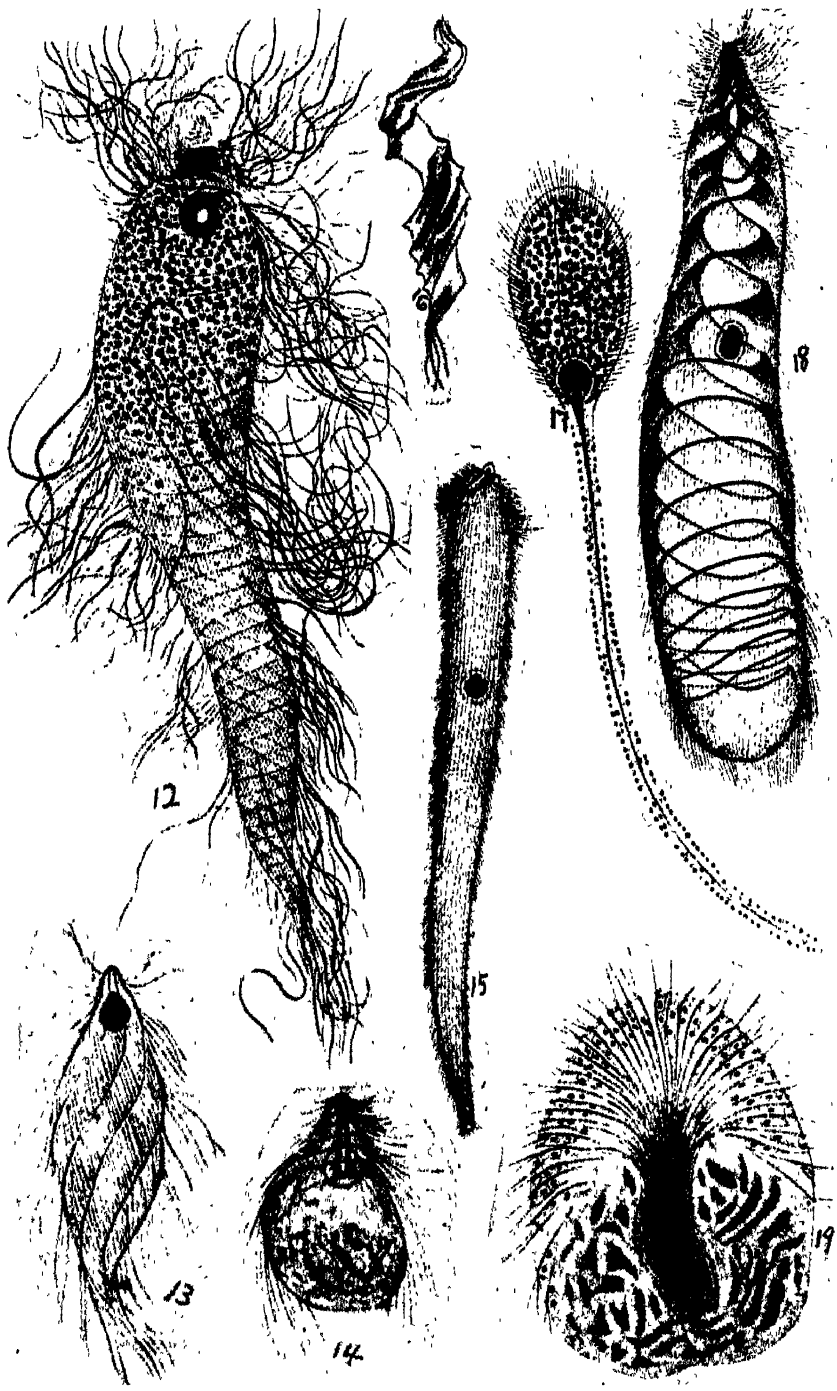


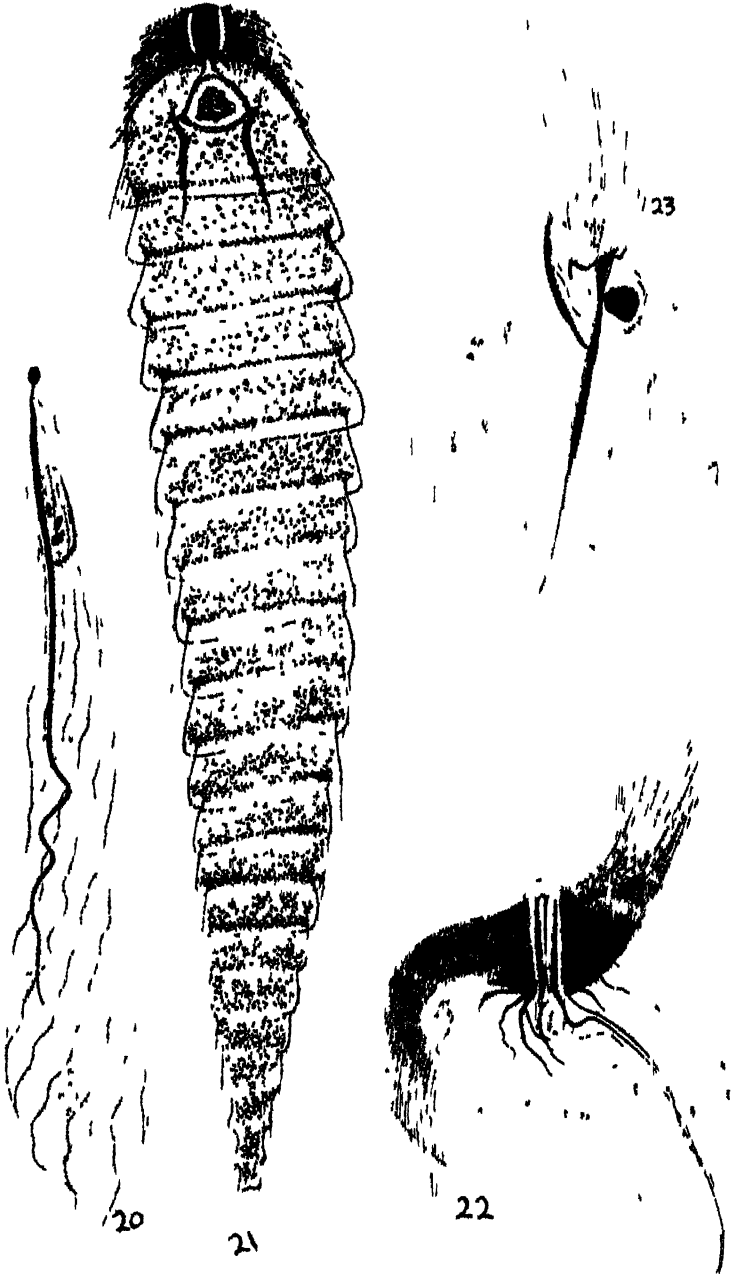
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EXPERIMENTAL STUDIES ON MORPHOGENESIS IN THE NERVOUS SYSTEM

By S. R. DETWILER

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THE application of the experimental method to the study of the developing nervous system has yielded results which have extended greatly our knowledge regarding certain aspects of differentiation. One of the outstanding achievements made by the use of this method was the solution of the well known question of the genesis of the nerve fiber. The neurone theory of His ('86, '87) and Forel ('87), which seemed incapable of being satisfactorily demonstrated by the method of direct observation, was given firm and conclusive support mainly through the experimental researches of Harrison ('04a, '06, '07a, '07b, '10a, '10b).

The question of the origin of the nerve fiber was first tested experimentally by Harrison ('04a, '06) and by Braus ('05). Harrison removed the ganglionic crest cells from frog embryos, and found that the embryos developed without sensory nerves and ganglia, but that motor nerves were present. These were devoid of sheath cells. He also showed that, when the ventral half of the embryonic spinal cord was removed, but with the dorsal part of the cord and ganglionic crest cells intact, the larvae were devoid of the motor nerves. His results clearly indicated that the nerve fiber does not have its origin in the sheath cells, but that it grows out from a single ganglion cell, with which it remains in continuity throughout life. A full account of researches on the histogenesis of the nerve

fiber has recently been published by Harrison. (Jour. Comp. Neur., vol. 37, 1924.)

Braus made the interesting discovery that the amphibian limb rudiment has the ability to undergo differentiation independent of its normal organic environment ('04), and that when transplanted to an abnormal situation it may acquire nervous connection with the central nervous system of the host and even exhibit spontaneous movements. He took advantage of limb grafting as an experimental method for the study of a number of fundamental questions concerning the development of the nervous system. He did not believe that the nerves, which developed within a transplanted extremity, grew in from the central nervous system of the host, but that the peripheral portions of the nerves developed *in situ* within the appendage and secondarily made connections with the nervous system of the host. Although all of Braus' experiments were ingenious in type, he endeavored to support Hensen's ('64) protoplasmic bridge theory, according to which protoplasmic bridges are supposed to be left everywhere between dividing cells of the embryo, so that when nerves begin to differentiate there is a complex system of protoplasmic connections within the organism. Those which function as conduction pathways are supposed to differentiate into nerve fibers, whereas the remainder ultimately disappear.

Banchi ('06) also carried out limb

transplantation experiments in connection with the question of nerve origin and likewise interpreted his results in support of the Hensen theory. In the limb grafting experiments of Harrison ('07a) and Gamelli ('06), evidence was brought to bear against the Hensen theory, and the outgrowth theory was given valuable experimental support. Whereas Braus claimed that aneurogenic limb buds (those taken from nerveless larvae) did not acquire nervous connection with the host—since they were disconnected from the nerve centers during the critical period, Harrison's experiments showed that aneurogenic as well as eneurogenic limb buds (those taken from normal larvae) became supplied with peripheral nerves. Harrison made a much more crucial experiment in grafting a limb rudiment from a normal embryo to one which had previously been deprived of its central nervous system. In such cases the developing appendage was devoid of nerves. This indicated, therefore, that nerves which develop within a grafted appendage, grow into it from the central nervous system of the host.

Whereas the results of Harrison's limb grafting experiments left little doubt in the minds of most neurohistologists as to the validity of the outgrowth theory, nevertheless, the advocates of the Hensen school still demanded more rigorous proof. This was soon after furnished by the tissue culture experiments of Harrison ('10a) in which he explanted neuroblasts of frog embryos into clotted lymph and observed with the eye the developing nerve as a protoplasmic outgrowth from a single ganglion cell, a concept which had already gained considerable footing through the careful investigations of His ('86, '87, '88, '90), Ramón y Cajal ('90, '92, '94, '06) and v. Lenhossék ('92, '95, '06).

Harrison's results were corroborated by Burrows ('11) and Lewis ('11) and the 'neurone' as the genetic and morphological unit of the vertebrate nervous system became firmly fixed. With the establishment of this concept great attainments have been made in the fields of nerve regeneration and transplantation, and our knowledge of reflex pathways has grown rapidly.

THE INFLUENCE OF THE PERIPHERAL FIELD ON NEURON DEVELOPMENT

Although it seemed clear from the experiments on explantation of primitive ganglion cells, that the initial outgrowth of the nerve fiber can proceed from the neuroblast independently of any functional requirements on the part of the endorgan, no especial attempt was made in these experiments to study the effects of normal organic stimuli upon the extent of neuron differentiation. The results of experiments directed towards the solution of this question (Braus, '06; Burr, '16a; Dürken, '11; Shorey, '09, '11) indicated that in the absence of certain peripheral areas, the nerve centers normally supplying those areas undergo hypoplastic development, supposedly from the lack of the peripheral functional demands which normally activate their complete development. Braus (op. cit.) found as a result of excision of the forelimbs of *Bombinator* prior to the outgrowth of the brachial plexus, that the plexus in larvae preserved ten days after the operation was as well developed as the normal, and that no reduction in the size of the ventral horn areas could be detected. Observations, however, on operated larvae, which were kept alive until just before metamorphosis, showed that the brachial plexus was reduced in size, as were also the ventral horn areas ordinarily supplying the limb. Braus

interpreted his results in accordance with the general developmental theory of Roux ('85) in stating that the development of the central nervous system can be divided into two periods: the first, in which growth and differentiation are independent of functional activity; and the second, in which further differentiation and growth continue only under the influence of this factor.

Miss Shorey ('09) carried out extirpation experiments on the limb rudiments of *Amblystoma* and the chick, and claims

plied in the culture medium. As a result of her observations she concluded that motor nerve growth is not only entirely dependent upon the presence of muscles, but that no neuroblasts can differentiate unless under the stimulus supplied by the functional endorgan or the metabolic products of the same. On the basis of her observations she opposed Harrison's conclusions that the outgrowth of the nerve fiber can proceed independently of any functional requirements on the part of the endorgan.

TABLE I

Showing the effects of removal of the limb and the activity of the transplanted limb upon the development of peripheral afferent

GANGLION CONNECTED WITH NORMAL INTACT LEFT LIMB			GANGLION WITH RIGHT LIMB REMOVED			GANGLION CONNECTED WITH RIGHT LIMB TRANSPLANTED TO A HETEROLOGIC POSITION			GANGLION NOT CONNECTED WITH EITHER LIMB			RATIOS	
Number of spinal ganglion	Number of cells counted	Weight of the model in grams	Number of spinal ganglion	Number of cells counted	Weight of the model in grams	Number of spinal ganglion	Number of cells counted	Weight of the model in grams	Number of spinal ganglion	Number of cells counted	Weight of the model in grams	Cell number	Weight
3	1,725	30.4841	3	850	12.9748							0.492	0.425
4	1,430	26.1604	4	685	9.7311							0.479	0.372
5	955	16.8798				5	1,195	22.2939				1.25	1.32
						6	1,171	26.5422	6	693	12.6600	1.69	2.09
						7	1,084	21.7634	7	720	11.7366	1.51	1.85
									9*	754	15.5456		
									9†	773	17.2328	1.02	1.10

* Left ganglion.

† Right ganglion.

to have found marked deficiencies in the peripheral nerves as well as in the ventral horn areas subsequent to the removal of the appendicular musculature. Also, the degree of the defect was said to be more or less proportional to the extent of the peripheral destruction. In a later work ('11) in which she explanted neuroblasts in a variety of culture media, she claimed that axone outgrowth ensued only in those cases in which beef extract (metabolic products of muscle) was sup-

HYPERPLASIA IN SENSORY GANGLIA

It was in connection with the above question that the original limb experiments of the writer (Detwiler, '20a, '20b) were carried out. Rather than to test the effects of the destruction of peripheral areas on the developing neurones, experiments were devised to test whether or not, by overloading the periphery at a given region, the corresponding peripheral neurones can be induced to undergo hyper-

normal (hyperplastic) development to meet the added functional requirements imposed upon them. Accordingly, the right anterior limb rudiment of *Amblystoma* embryos was transplanted in the same embryo and at distances varying from one to seven somites caudal to the normal situation (autoplastic grafts). In this way it became possible to study the effects of the development and function of limbs so placed upon the neurones supplying them. Observations on the functional responses of the transplanted limbs as well

cord just posterior to the original limb levels (sixth, seventh and eighth segments). The nerves of these levels normally supply afferent fibers to the body integument and efferent fibers to the muscles of the body wall. Throughout these experiments there was evident a marked tendency for the transplanted limbs to receive innervation from the normal limb levels of the cord.

The most instructive cases of the limb experiments were those in which the limbs were shifted caudally the distance of four

TABLE 2

Showing number of cells counted in twenty consecutive transverse sections of the right half of the spinal cord at the levels of the third, fourth, and fifth segmental nerves respectively (anterior limb levels)

CONDITIONS	CASES	III NERVE LEVEL	IV NERVE LEVEL	V NERVE LEVEL	CELLULAR RATIO BETWEEN III AND V NERVE LEVELS
Normal.....	AS ₄	3464	2796	2346	III:V 1.48:1.00
Limb excised, spinal cord intact.....	AS ₄₃₈	3904	2803	Connected with limb 2352	1.66:1.00
Seventh, eighth, and ninth spinal segments substituted for the third, fourth, and fifth, respectively	TrSC ₁₃₇ *	3130	2600	2500	1.25:1.00
	TrSC ₁₃₈ *	3043	2973	2728	1.11:1.00
Limb level of spinal cord (third, fourth, and fifth segments) reversed	ReSC ₁ †	3500	2593	2215	1.62:1.00
	ReSC ₁₀ †	3265	2809	2326	1.40:1.00

* In cases TrSC₁₃₇ and TrSC₁₃₈, the third, fourth, and fifth nerve levels represent, respectively, the transplanted seventh, eighth, and ninth.

† In cases ReSC₁ and ReSC₁₀, the third nerve level represents the reversed fifth, whereas the fifth nerve level represents the reversed third.

as the segmental nerve supply have been published previously in tabular form (Detwiler, '20b, tables 1 and 2). It may not be redundant here to state that limbs which were transplanted from one to three segments caudal to the normal position were found to receive nearly their entire nerve supply from the original limb levels of the cord (third, fourth, and fifth segments). Limbs which were transplanted a distance of more than three body segments caudal to the normal position received the bulk of their nerve supply from segments of the

body segments (fig. 15). Limbs so placed were typically found to be innervated from a plexus composed of the fifth, sixth, and seventh segmental nerves, the fifth of which is a normal limb nerve. Limbs so innervated exhibited a high degree of activity which was coordinated with the contralateral extremity. Microscopical examination of such cases showed that the strange segmental nerves (sixth and seventh) contributing to the grafted limb were larger than the contralateral nerves which had, of course, no connection with

a limb. This enlargement was found to be due to a hyperplasia of the sensory neurones. Evidence of sensory hyperplasia was not only suggested by the obvious differences in the size of the spinal ganglia (figs. 13, 14) and the posterior roots, but was also quantitatively estimated by making a numerical count of the sensory ganglion cells (table 1).

Excision of the limb rudiment was also found to result in a 52 per cent hypoplastic development of the sensory neurones of the limbless nerves (table 1). From the fact that the percentage of weight reduction in the posterior roots exceeded that of the ganglia, the results also indicated that in addition to a hypoplasia, a slight atrophy of the afferent neurones ensued. No exact quantitative observations have been made on the size changes in the sensory neurones disconnected with the normal limb or in those connected with a transplanted limb.

As striking as the sensory responses have been to decreases and increases in the peripheral field, no experiments have as yet been completed to ascertain at what period in the development of the embryo these reactions set in or terminate, though investigations concerning these questions are under way. Furthermore, the question as to whether the sensory hyperplasia in nerves connected with a transplanted limb is entirely related to the integumentary increase is one which also needs investigation. An analysis of this situation meets with difficulty since when spinal nerves are brought into relation with a transplanted limb, they not only have a greater integumentary area to supply, but by reason of the added musculature (limb and shoulder muscles) it is reasonable to expect that there should be an augmentation in the number of proprioceptive fibers to the muscles. Since it has been impossible to distinguish between pro-

prioceptive and exteroceptive neurones, it is difficult to say how much of the hyperplasia in the ganglia can be ascribed to integumentary increase. It may be possible, however, to analyze the situation further as a result of experiments which are under way. These have been devised in a way to diminish the integumentary area on the embryo without affecting a diminution in the musculature. By so doing it may be possible to obtain a rough estimate of the part played by exteroceptive and by proprioceptive neurones in hyperplased ganglia connected with a limb.

Whereas the limb transplantation experiments have shown a marked sensory reaction (hyperplasia) to the peripheral overloading, no evidence as yet of a similar response on the part of the efferent neurones has been obtained either from a comparative study of the motor roots or from a numerical comparison of the motor nerve cells in both halves of the spinal cord at the levels involved. Neither as a result of the excision of the limb was there any measurable evidence of a hypoplastic development of the efferent fibers in the limb nerves ('20a, '23a), though such nerves actually did suffer a reduction in size.

A study of size changes in the primary brachial motor neurones following limb excision in *Amblystoma* embryos has recently been made (Detwiler and Lewis, '25) with the interesting observation that bilateral excision of the anterior limb rudiments causes a greater reduction in the size of the primary brachial motor neurones than when only one limb is excised. In the latter case the average area of the median plane of section of the motor horn nuclei (as estimated by the polar planimeter) shows a reduction of 8 per cent. The volume reduction of the motor roots is 24 per cent. Following bilateral ex-

cision of the limb rudiments the average area of the median plane of section of the motor horn nuclei shows a reduction of 20 per cent and the volume reduction in the motor roots is 32 per cent.

These results suggest that the size of the efferent neurones, in addition to being affected by the completeness of their functional connection with the peripheral field, is also dependent upon reflex connection with local commissural neurones of the opposite side of the cord. The exact way in which commissural neurones influence growth in the motor horn cells on the opposite side of the cord we are not yet in a position to state. The results indicate, however, that growth and function in groups of neurones may affect growth processes in others regardless of whether or not the latter be fully or only partly in connection with the peripheral field.

From the observed facts that proliferation in the primary brachial motor neurones is apparently unaffected by the excision of the limb rudiment, and that efferent neurones from atypical regions of the spinal cord fail to undergo hyperplastic reactions when in connection with a terminally increased musculature (transplanted limb), it is obvious that the extent to which brachial efferent neurones shall develop is not primarily under the control of the peripheral musculature. This conclusion is not in correspondence with the results of Miss Shorey's experiments, nor with the reflex circle idea of Bok ('17). Vermuelen (communicated by Bok) also reports a human monster in which a duplication of the tongue musculature was accompanied by a duplication of the hypoglossal nuclei in the brain stem. It is difficult to harmonize the observations of Vermuelen and Bok with my own results. It would seem that if increased functional activity on the part of the

peripheral musculature had any effect upon proliferation of motor neuroblasts, manifestations of a definite sort should be forthcoming in the limb transplantation experiments, yet in no case so far studied, whether the transplanted limb was large or small, functional or useless, single or double, has there ever been found measurable evidence of motor hyperplasia such as has been almost without exception on the part of the sensory nerves.

The limb grafting experiments have indicated clearly then that the principal agencies involved in neuroblastic proliferation of sensory and of motor nerves are not the same, and that factors other than the functional activity of the end organ must combine in determining the extent of motor cellular differentiation within the spinal cord.

PROLIFERATION OF CELLS IN THE CENTRAL NERVOUS SYSTEM

It was suggested as a result of the limb experiments that if the extra-limb segments of the cord, which are capable of producing only limited movements in transplanted limbs, could be substituted for the limb region of the cord, it would present a condition whereby it would be possible to study more favorably the ability of such extra-limb segments to execute normal movements when in connection with the proper central reflex pathways. Also the substituted portion of the cord would be subjected to all the stimuli which normally produce the typical proliferation of nerve cells in this region.

Experiments were then carried out in which the anterior limb region of the spinal cord (third, fourth, and fifth segments) were excised and replaced by a more caudal unit comprising the seventh, eighth, and ninth segments from another embryo ('23a). A typical example of

such a case with a composite spinal cord is shown in figure 18. A complete report of these experiments has been published elsewhere (Detwiler, '23a) and reference to them will be made here only in so far as they bear upon the questions under consideration. Aside from the fact that in 50 per cent of these cases with composite spinal cords, normal limb activ-

mental animal are shown in figures 1 and 2 respectively. From figure 1 it is seen that throughout the spinal cord from the level of the third nerve to the level of the ninth there is a gradient of cellular proliferation which diminishes down the cord. In the experimental case (fig. 2) the same is to be noted, yet here the greater cellular proliferation character-

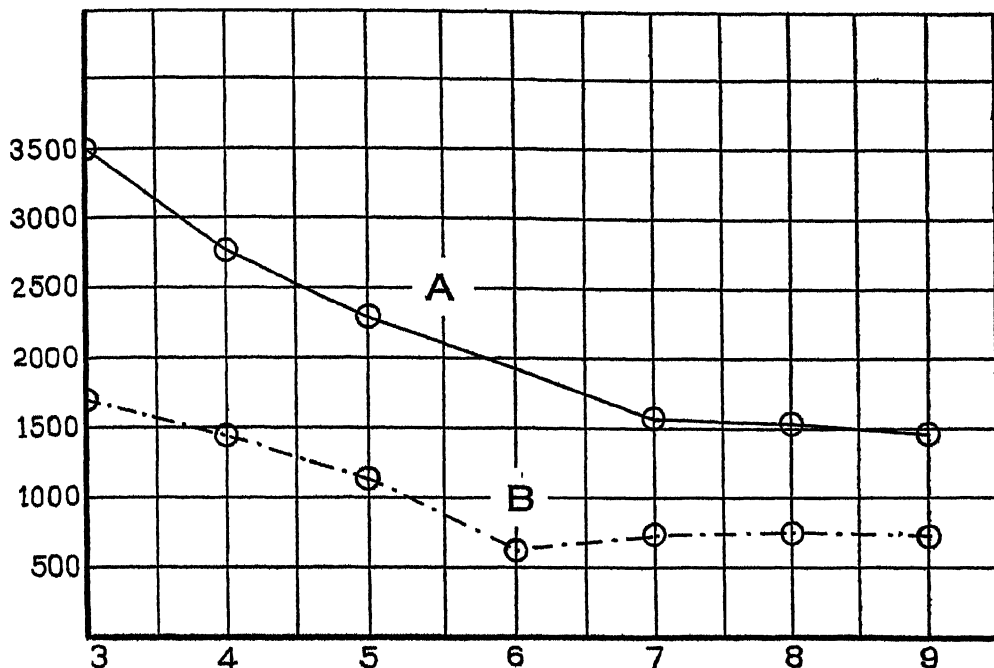


FIG. 1. GRAPH SHOWING THE EXTENT OF CELLULAR PROLIFERATION WITHIN THE RIGHT HALF OF A NORMAL SPINAL CORD FROM THE LEVEL OF THE THIRD NERVE TO THE LEVEL OF THE NINTH (CURVE A), AND THE EXTENT OF SENSORY PROLIFERATION IN THE CORRESPONDING SPINAL GANGLIA (CURVE B)

Abscissae designate the respective spinal segments (three to nine); ordinates represent in Curve A, the number of cells counted in twenty consecutive transverse sections of the spinal cord at the levels of each nerve, and in B, the number counted in each corresponding right ganglion. The third, fourth, and fifth segments are normally connected with the limb.

ities ensued, it was found that the grafted segments of the cord in their new situation (anterior limb region) underwent an increased cellular proliferation approximately equal in extent to that which characterizes the normal anterior limb levels. The results of a cellular count from the spinal cord of a normal larva of approximately fifty days of age and from an experi-

menting the anterior limb region of the cord (third, fourth, and fifth segments) as compared with the more caudal region has proceeded from a unit of cord which typically occupies the caudal position (seventh, eighth, and ninth segments).

Since extirpation of the anterior limb was found to have no effect upon cellular proliferation in the cord ('23a), the

marked hyperplasia observed in the grafted unit of spinal cord appears to have no primary relation to the appendicular musculature. This conclusion has received further support from a series of experiments in which a cellular hyperplasia of similar magnitude occurred in the grafted unit of cord in the absence of the limb ('24).

In a theoretical discussion of these

justified as a result of experimental end-for-end reversal of the limb region of the spinal cord (third, fourth, and fifth segments) which resulted in the development of a normal pattern of the spinal cord and peripheral nerves from the inverted segments (Detwiler, '23b).

Under normal conditions more nerve cells develop in the third segment than in the fifth. Under the experimental

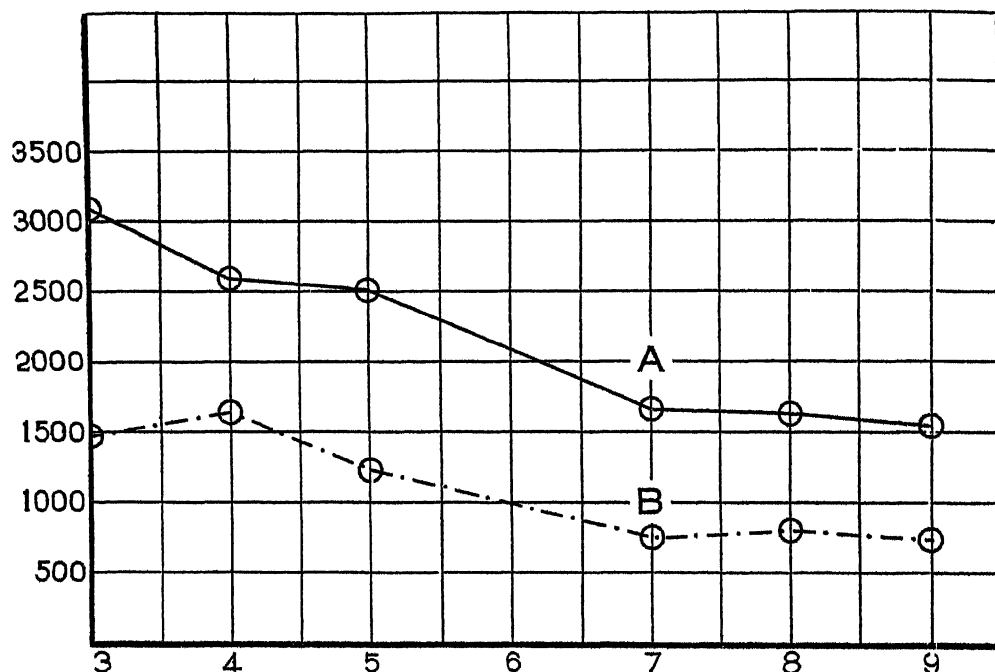


FIG. 2. GRAPH SHOWING THE EXTENT OF CELLULAR PROLIFERATION WITHIN THE RIGHT HALF OF THE SPINAL CORD (CURVE A) AND IN THE RIGHT SPINAL GANGLIA (CURVE B) IN EXPERIMENTAL CASE TrSC₁₃₇

Normal anterior limb region of the cord excised (third, fourth, and fifth segments) and replaced by the seventh, eighth and ninth segments from another embryo. Abscissae and ordinates as in figure 1.

results it was suggested that the increased cellular proliferation in the transplanted seventh, eighth, and ninth segments in their grafted position may be the result of their being under the influence of a greater number of central longitudinal pathways descending from higher levels, such as the fasciculus longitudinalis medialis and the tractus bulbospinalis (Herrick, '14). This viewpoint seemed further

conditions the fifth segment, which occupies the position of the third, is found to undergo hyperplastic development similar to the normal third, whereas the third segment when moved caudally to the position of the fifth, undergoes decreased proliferation so as to typify the normal fifth segment (table 2).

From the constancy in the extent of proliferation within the various seg-

ments of the limb region of the cord under both experimental conditions, the accumulated evidence seems to bear out the idea that the degree of proliferation which is reached in these levels of the cord is commensurate with the number of longitudinal conduction fibers normally terminating therein for the coordinate control of the appendicular reflexes. If such were the case is it possible that we have here an exemplification of the "Stimulogeneous Fibrillation" concept of Bok ('15)? Bok's theory was founded on observations from normal development, and forms much of the anatomical foundation for Kappers' ('17, '21, '22) theory of neurobiotaxis.

It is of course difficult to say whether the cellular increases observed are actually the result of the stimulative influence of a greater number of internal fiber tracts entering these higher levels or whether such increases can be referred partly or entirely to the influence of the axial physiological gradients as suggested in the work of Child ('21), Bellamy ('19) and others.

Coghill ('23, '24b) has shown from an exhaustive study of nervous development in *Amblystoma* (non-motile, early flexure, coil and early swimming stages) that there are localized regions where differentiation and proliferation of cells take place according to a very definite pattern, and that acceleration of these processes in different regions of the central nervous system is definitely related to the development of the behavior pattern. He further shows that one process tends to become accelerated where the other is retarded, and that both take place in the form of waves which probably pass cephalocaudad through the brain and spinal cord. His work is of great importance since it distinguishes in a quantitative way between the two processes of proliferation

and differentiation of the nervous elements. He has clearly brought out fundamental morphological differences between the two as well as the general physiological significance of these two phases of growth. His observations afford convincing evidence that in early stages of development, the resolution of indifferent cells into neuroblasts, the early proliferation of these neuroblasts and the regional localization in the acceleration and retardation of these processes are accomplished under influences which precede any activating stimuli which may come from ingrowing nerve roots and tracts. These more elementary influences seem to be bound up with the hereditary organization of the protoplasm and the primary physiological gradients.

In referring to the cellular hyperplasias which were observed in the transplanted spinal segments described in my spinal cord experiments ('23a), Coghill suggests that injury inflicted during the grafting may have played some part in the extensive proliferation observed. He calls attention to Hooker's ('15) observations on the healing processes in transected spinal cords of *Amblystoma* and *Rana*. Hooker observed a rapid proliferation of cells in the vicinity of the wound seven days after the operation. In a later work Hooker ('23) reported that injuries to the cord produce proliferation by mitosis of the cells of the mantle layer. Coghill's suggestion, therefore, partly rests upon Hooker's observations.

A full discussion of this matter is taken up in a separate paper (Detwiler, '25c) in which it is shown that injury inflicted during the grafting in the spinal cord segments probably plays no significant role in the observed hyperplasias. In this connection the experiments dealing with the end-for-end reversal of the limb region of the cord are instructive. Here

the third segment has been replaced by the fifth and the latter in turn has been replaced by the third. Reference to table 2 will show that the number of cells counted in the transplanted third segment in both cases was slightly lower than in the normal fifth, and in the transplanted fifth segment the number (case ReSC 10) is approximately 200 less than in the normal third. From the fact that in three instances out of four transplanted segments, proliferation is slightly less than that characterizing the normal, injury must be looked upon as being an ineffectual factor in the results. The same applies to the experiments in which the first five segments of the cord were excised and replaced by a unit of central nervous system consisting of the medulla and the anterior two segments of the cord (Detwiler, '25a). Here the transplanted medulla underwent hypoplastic development whereas the spinal portion of the graft underwent hyperplastic development. Since both parts of the graft were subjected to the same injury it is difficult to imagine any significant effects due to this factor.

The data at hand indicate, therefore, that hyperplasias occurring in grafted units of spinal cord cannot be ascribed to the stimulating effects of injury.

Coghill ('24b) shows (his figs. 7 and 8) that in early stages of development in *Amblystoma*, cell proliferation and differentiation are associated in the growth of the spinal cord. He finds that the seventh, eighth, and ninth segments which I transplanted into the brachial region, and which underwent marked hyperplasia, fall well within the range of relatively high potentiality of both proliferation and differentiation. Since the tenth, eleventh, and twelfth segments fall beyond the limits of so great a potentiality, Coghill raises the question as to whether these

latter segments would have the same capacity for growth in the brachial region as did the seventh, eighth, and ninth. Herrick ('25) also calls attention to this point and he says (page 122):

It should be borne in mind, however, that Coghill has shown in *Amblystoma* larvae of the stages immediately subsequent to those upon which Detwiler operated, the third, fourth and fifth segments of the cord are in a field of rapid cell proliferation which seem to be an expression of cephalo-caudad pulses of growth whose underlying causes have not yet been determined, and the matter evidently needs further investigation.

He further says,

The relative part played here by the primary physiological gradients and the influence of ingrowing fiber tracts remains to be determined.

This question is open, at least in part, to an experimental analysis which will form the subject of future investigations. By comparing proliferation in the tenth, eleventh, and twelfth segments with that in the seventh, eighth, and ninth, both under normal conditions and when transplanted into the more cranial positions, greater possibilities will be afforded to determine more definitely than hitherto the extent to which various agencies are affecting the normal growth processes.

In further consideration of the possible stimulative effects of fiber ingrowth upon cellular proliferation, attempts have been made to disconnect descending bulbar tracts from the spinal cord by interposing, in the developing embryo, mechanical obstacles such as thin sheets of celloidin between the medulla and the cord. It was the purpose to test out whether in the absence of the invasion of such tracts into the cord, proliferation therein would suffer incompleteness. These experiments so far have been unsuccessful.

Recently I have published the results of a series of experiments ('25a) in which

a marked influence of the medulla on proliferation in the anterior end of the cord was obtained. Advantage was taken of Herrick's ('14) observations that in *Amblystoma* certain descending tracts arise in the motor tegmentum of the medulla and pass into the ventral funiculi of the same and the opposite sides of the cord (bulbo-spinal tracts). It was designed here to augment the possible stimulating effects of such descending fibers by interpolating an additional medulla just caudal to the normal.

In these experiments the first five segments of the cord were excised and replaced by a unit of central nervous system including the caudal end of the medulla and the first two segments of the cord. Under the new conditions the first three segments of the cord are replaced by the extraneous medulla and the fourth and fifth segments are replaced by the grafted first and second (figs. 3, 4).

The results of these experiments showed a more extensive proliferation of cells in the spinal segments just caudal to the transplanted medulla than occurs under normal conditions. The cellular increase was most marked in the transplanted first and second segments and became less marked in successive segments (cf. figs. 5 and 6). The cellular increases in the grafted cord segments have been looked upon as resulting from the added stimulative effects brought about by the augmentation in the descending bulbar tracts arising in the extraneous medulla, and passing ventrally into the cord.

In discussing the question of the action of gradients in the process of growth, Herrick ('25) has looked upon this cellular increase in the cord as being the direct result of the introduction of a new center of dominance into an atypical place.

The general interpretations which were made as a result of the medulla trans-

plantations became subject to certain modifications in consequence of further experiments (Detwiler, '25d). These involved the removal of the fourth, fifth, and sixth segments of the spinal cord and replacing them by a unit of cord comprising the first three segments from another

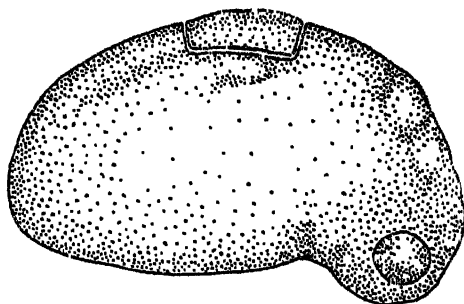


FIG. 3. OUTLINE DRAWING OF *Amblystoma* EMBRYO, SHOWING REPLACEMENT OF FIRST FIVE SEGMENTS OF THE SPINAL CORD BY A UNIT OF NEURAL TUBE COMPRISING THE MEDULLA AND THE FIRST TWO SPINAL SEGMENTS FROM ANOTHER EMBRYO. X 10

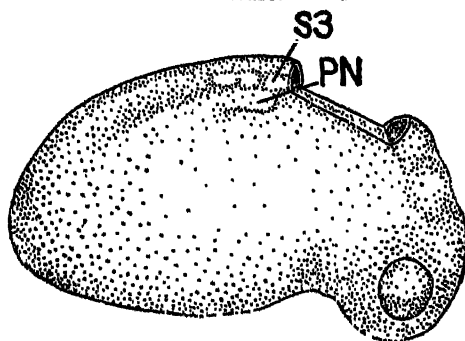


FIG. 4. OUTLINE DRAWING OF *Amblystoma* EMBRYO, SHOWING EXCISED REGION (MEDULLA AND FIRST TWO SPINAL SEGMENTS) WHICH WAS GRAFTED TO EMBRYO SHOWN IN FIGURE 3. X 10
S3, third somite; PN, pronephros

embryo (fig. 20). In several cases the third, fourth, and fifth segments were excised instead of the fourth, fifth, and sixth. Under the new conditions the grafted first and second segments of the cord occupy the positions of the fourth and fifth respectively. This position of the transplanted first two

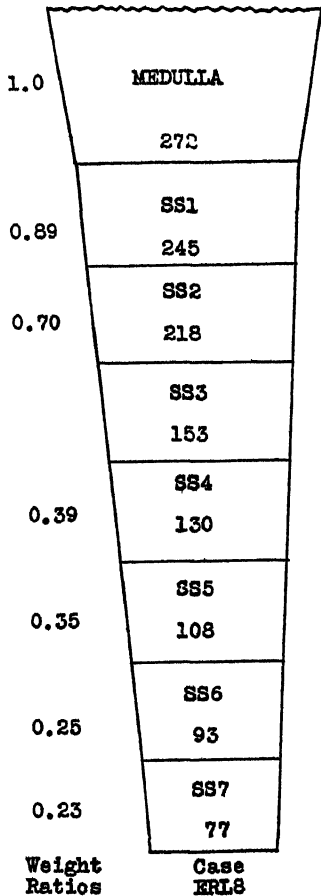


FIG. 5

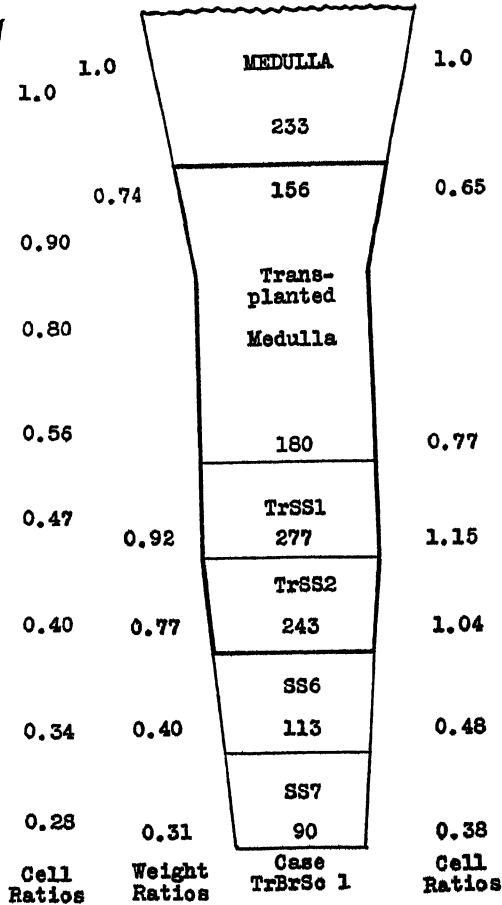


FIG. 6

FIG. 5. A DIAGRAMMATIC PLAN OF THE CELLULAR REGION OF THE CENTRAL NERVOUS SYSTEM OF A NORMAL *Amblystoma* LARVA FROM THE LEVEL OF THE ACOUSTIC (EIGHTE CRANIAL) NERVE TO THE CAUDAL LIMIT OF THE SEVENTH SPINAL SEGMENT

The central figures express the average number of cells per section as obtained by counting the number in the right halves of ten consecutive transverse sections through a known region for each segment represented. The weight ratios are based on the weights in grams of unassembled wax models of thirty consecutive transverse sections through the medulla and the various spinal segments indicated. SS1-SS7, first seven spinal segments.

FIG. 6. A DIAGRAMMATIC PLAN OF THE CELLULAR PORTION OF THE CENTRAL NERVOUS SYSTEM OF *Amblystoma* LARVA TrBrSc 1, FROM THE LEVEL OF THE ACOUSTIC (EIGHTE CRANIAL) NERVE TO THE CAUDAL LEVEL OF THE SEVENTH SPINAL SEGMENT

The first five segments of the spinal cord were excised and replaced by a unit of neural tube comprising the greater portion of the medulla and the first two spinal segments (TrSS1 and TrSS2). The added medulla occupies the region of the normal first, second and third spinal segments. The transplanted first and second segments occupy the position of the fourth and fifth, respectively (v. fig. 3). The central figures express the average number of cells per section as obtained from counting the number in the right halves of ten consecutive transverse sections through the same regions as used in the study of the normal individual (cf. fig. 5). Weight ratios obtained in the same manner as outlined in explanation of figure 5. TrSS1 and TrSS2, transplanted first and second spinal segments; SS6 and SS7, normal sixth and seventh segments.

spinal segments corresponds to that occupied by them in the former experiment involving the medulla ('25a). The difference lies in the fact that in one case the transplanted segments are preceded by an extraneous medulla, whereas in the other, they are preceded by the normal anterior three segments of the cord.

The results have shown that the anterior end of the cord (first and second segments)

ventral regions (cf. figs. 7 and 8). Moreover, the cellular proliferation in the intact spinal segments cephalad to the transplanted ones was found to be markedly increased, particularly throughout the dorsal regions, which are predominately sensory, and to such an extent that the shapes of these anterior intact segments simulated that of the caudal end of a normal medulla. The striking change

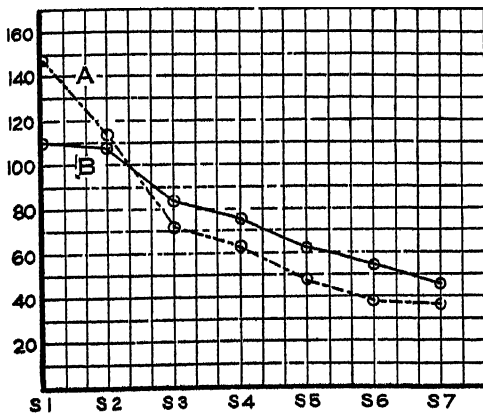


FIG. 7. Curve showing extent of cellular proliferation throughout the dorsal half (curve A) and the ventral half (curve B) of the spinal cord from the level of the first spinal nerve to the level of the seventh in a normal *Amblystoma* larva. Abscissae represent respective spinal nerve levels (1 to 7). Ordinates represent the mean number of cells counted in ten alternate sections through each nerve level. For further explanation v. Detwiler '25d.

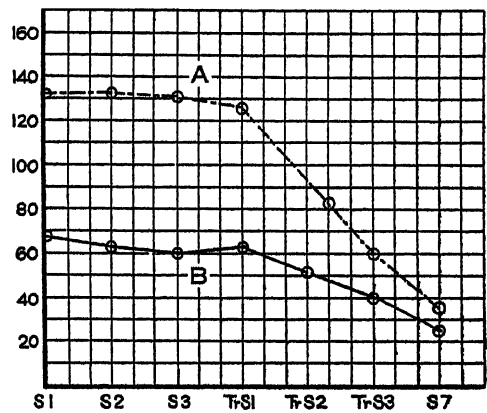


FIG. 8. Curve showing extent of cellular proliferation throughout the dorsal half (curve A) and ventral half (curve B) of the spinal cord from the first to seventh nerve levels in experimental case TrSC₂₃. The fourth, fifth, and sixth segments of the spinal cord were replaced by a unit of cord comprising the first three segments from another embryo. Abscissae indicate respective spinal nerve levels (1 to 7). Ordinates indicate mean number of cells counted in ten alternate sections through each nerve level.

when moved caudally in the embryo does not decrease in cellular proliferation to such an extent as was found in the case of the spinal cord reversal experiments involving the anterior limb region ('23b). The transplanted segments approach their typical size and normal cellular proliferation in the more caudal position. The proliferation of cells in the transplanted segments was found to take place more extensively in the dorsal than in the

in the difference between proliferation throughout the dorsal and the ventral regions of the transplanted segments as compared with the normal, suggests that in these segments capacity for self-differentiation is much higher in the dorsal portion of this region of the cord.

Cellular hyperplasia throughout the dorsal region of the intact anterior segments of the cord under the experimental conditions points to a stimulative influ-

ence exerted upon these regions by the transplanted segments lying caudal to them. This influence is seen to be effective only throughout the dorsal regions.

It would appear from the character of the results that there exists in the dorsal region of the anterior segments of the cord, particularly in the first and second segments, sensory centers inherently of

strong sensory pathways (spinobulbar) are developed cephalad into the brain.

If these results are viewed from the standpoint of the effects brought about through the influence of growing axones, it would seem that there are two main influences affecting the final proliferation in the anterior segments of the cord. These seem to show a correspondence with

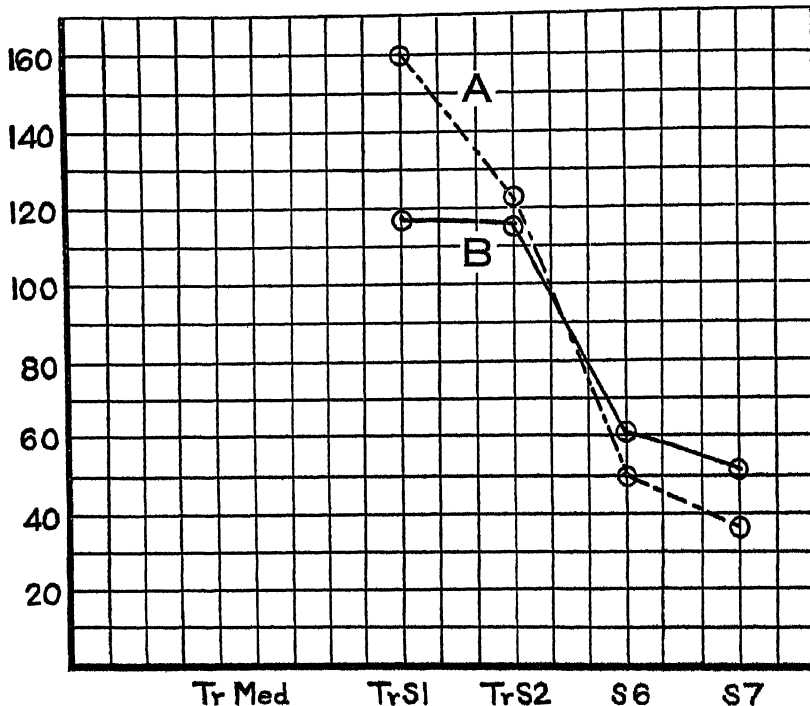


FIG. 9. GRAPH SHOWING EXTENT OF CELLULAR PROLIFERATION IN THE DORSAL HALF (CURVE A) AND THE VENTRAL HALF (CURVE B) OF THE SPINAL CORD IN EXPERIMENTAL CASE TrBrSCI

First five segments of the cord excised and replaced by the caudal end of an extraneous medulla and the first two spinal segments from another embryo. The transplanted first and second spinal segments occupy the position of the normal fourth and fifth respectively. Abscissae and ordinates as in figure 7.

high capacity for proliferation and that a strong influence passes out from this center—particularly in a cephalad direction. The question has been raised previously ('25d) whether or not this influence may be associated with the extent to which ascending tracts arise in this region, for this region is one through which

the direction in which the principal pathways are growing. When the grafted anterior segments of the cord are preceded by an extraneous medulla, proliferation in the grafted segments is increased, but the relation between dorsal and ventral proliferation is essentially typical (cf. figs. 7 and 9). On the other hand, when

the anterior segments are transplanted to these same levels, but with the first three segments left intact, proliferation in the dorsal regions of the transplanted segments is disproportionately high. The same is true for the intact anterior segments (figs. 7 and 8). The fact that a normal dorso-ventral relationship results when the grafted spinal segments are preceded by an extra medulla, argues for a bulbar influence on these segments under normal conditions which is stronger ventrally than dorsally. Certainly the inherent capacity for extensive proliferation in the ventral regions of the anterior end of the cord is not as high as in the dorsal regions and only when preceded by an extraneous medulla does this ventral region proliferate in proportion to the dorsal.

How far these results can be brought in line with the action of gradients I am not yet in a position to state. If viewed from this standpoint, they indicate that in the sensory region of the anterior end of the cord, there exists a center of dominance with a physiological influence passing cephalad as evidenced by the cellular hyperplasias occurring throughout the sensory regions lying in front of the graft.

Although numerous agencies are at work in the embryological development of the nervous system (Herrick, '25), there appears to be no doubt from experimental evidence that there is a stimulative influence resulting from the growth of nerve fibers into a field in the process of differentiation.

In addition to the indications brought out in my own experiments, the work of Burr ('20, '23) offers corroboration in this connection. In his earlier work on the removal of the nasal placodes in *Amblystoma* embryos, Burr ('16a) found that the corresponding cerebral hemisphere failed to complete its development. Up

to the time when the nasal organ begins to function, the hemisphere on the operated side was as well developed as on the normal side. Since it failed to complete its development after that period, Burr concluded that the hemisphere receives a stimulation from the functional activity of the endorgan (nasal placode) which affects its complete development. In this connection he cited the results of Braus ('06) on the forelimb rudiments of *Bombinator*. Burr ('16b) found further that regeneration of the hemisphere failed in the absence of the olfactory placode, but ensued if the placode was left intact. Here it is evident that some influence from the peripheral organ is essential for the regeneration of the olfactory centers in the brain.

In a later work Burr ('20) came to the conclusion that some stimulus associated with the ingrowth of axones rather than the transmission of stimuli over already formed pathways influences cellular development in the hemisphere. In this connection Burr performed two series of experiments. In the first, the cerebral hemisphere with the adjacent olfactory placode was transplanted to a region just caudal to the right anterior limb and buried beneath the skin. In the second series, the same structures were transplanted to the same region but in this case the olfactory epithelium was healed into the skin and exposed to the exterior as under normal conditions, whereas the telencephalon was deeply buried. Burr found that the telencephalon was as completely organized in one type of experiment as in the other, indicating, therefore, no influence of a functioning end-organ on cellular production in the telencephalon. From his two types of experiments he concluded that the ingrowth of peripheral axones into the wall of the hemisphere was the important agent

influencing cellular proliferation in the hemisphere and not the functional activity of the end-organ. He strengthens his point of view by the observations that the ventral portion of the hemisphere which, by reason of the operation, is cut off from normal ascending fibers is much less differentiated whereas the dorsal portion, the function of which is entirely olfactory, is practically completely developed with the exception of the tracts connecting it with the rest of the brain. Burr says (page 165):

. . . . Hence it is reasonable to suppose that a part of the differentiation of the nucleus medialis septi and the primordium hippocampi is due to the ingrowth of centripetal fibers.

He says further

. . . . It is evident then that the factor which produces the second phase of nervous development in the telencephalon is not the functional activity of the nasal epithelium transmitted through the olfactory nerve, but rather the stimulus afforded by the actual ingrowth of neurones into the wall of the hemisphere.

It would be interesting, however, in connection with Burr's experiments to test out whether the olfactory epithelium which was exposed to the surface (second type of experiment) was actually capable of function, and, further, it would be important to know how far proliferation in the olfactory portion of a grafted hemisphere would proceed in the entire absence of an olfactory placode.

The part played by fiber ingrowth in cellular production receives more substantial confirmation in Burr's later experiments ('23) in which he transplanted an accessory nasal placode adjacent to the normal. Here he found that connections were established with the hemisphere and that the augmentation of olfactory fibers thus entering the hemisphere brought about a cellular hyperplasia in the olfactory territory of the same.

In an analysis of Burr's work, Herrick ('25) says

It may be inferred that the developing olfactory epithelium produces some soluble substance (hormone) which diffuses through the tissues and activates the cells of the adjacent brain wall to more rapid proliferation, or that differences in bioelectrical potentials in the ingrowing olfactory organ can cut across the very short distance between this organ and the brain and so stimulate growth in the latter, or that the permeability of the tissue has been modified in some other way.

Herrick (*op. cit.*) brings out the point that this influence which is exercised upon the developing brain by the rapidly growing peripheral sensory surface may be of much more generalized nature physiologically than a true nervous impulse and indeed may be some phase of the general physiological gradients or some allied kind of process, as he terms it.

Coghill ('24b) has shown that there is a correlation between neuroblastic proliferation in certain regions and axonal ingrowth into the same, but calls attention to the point that, since high rates of proliferation are complete before axonal ingrowth in that region has occurred, the ingrowth of the axones is not the cause of proliferation. His figure 6, page 85, shows that the great increase in neuroblastic proliferation (285.4 per cent) in the cerebrum of *Amblystoma* between the coil stage and the early swimming stage is simultaneous with the ingrowth of the olfactory and the optic nerves. In regard to this point he says, "It is conceivable that the accelerated differentiation in the cerebrum stimulates the ingrowth of the olfactory and optic fibers." He also calls attention to a correlation of the rapid differentiation of neuroblasts in the rhombencephalon at early periods with the ingrowth of the nerve roots.

It is clear from Coghill's work that there are factors other than the growth of nerve

roots which activate proliferation of neuroblasts in the early stages. Nevertheless, there seems to be abundant experimental evidence to suggest that in later stages, at least, cellular proliferation becomes more clearly correlated with fiber invasion, and in fact, may be primarily under the influence of this agent.

In some recent experiments on embryonic eye transplantation (May and Detwiler, '25) we have obtained results which are of especial interest in this connection. The eye was transplanted into a wound resulting from excision of the otic placode (fig. 19). Incidentally the olfactory placode was grafted along with the eye. Of 15 cases examined microscopically, the optic nerve was found to enter the IX-X ganglion in 4 cases, the unremoved portion of the VII-VIII ganglion in 3 cases, and in 1 case it entered the medulla. The ingrowth of the axones into these nerve centers brought about a hyperplasia ranging from 22 to 52 per cent of the normal.

The exact manner in which axones growing into a region undergoing differentiation brings about increased cellular production is difficult of analysis. There seems to be at present no valid objection to interpreting the results in line with Cajal's neurotropism theory. Coghill ('24a) brings out the fact that nerve cells grow while they function and suggests that the power of one neurone to activate growth processes in another has origin in the growth phase rather than in the conduction phase of its metabolism. He cites in this connection the experiments of Harrison ('04b) in which he narcotized frog embryos in a 0.02 to 0.03 per cent solution of chloretone during the period when the early nervous pattern is being laid down and found that, upon removal, at a period five days later, they were able to complete normal swimming move-

ments in the course of about five minutes. Certainly this type of experiment argues for an influence other than that brought about through nervous conduction. Recent unpublished experiments by Matthews in the Harvard laboratory show that embryos narcotized for a period of fifteen days undergo a greatly retarded differentiation but that complete recovery of normal reflexes is realized in some cases, although the recovery period is considerably longer than when narcotized for shorter periods of time. It would appear from the character of the results that the delay in recovery results from the prolonged lowering of the growth potentials, though there is, as yet, no quantitative data in this connection.

The action of sensory fibers in bringing about the formation of sensory elements with which they are later in intimate contact, either through contiguity or continuity has been observed in normal development and also in regeneration. Szymonowicz ('95, '96) stated that both in the case of the corpuscles of Merkel and in the corpuscles of Grandy and Herbst, the differentiation of the sense organ is dependent upon the nerve. In the taste buds of fishes (Landacre, '07) and in those of man (Marchand, '02), it appears that the gustatory nerves are the elements which cause differentiation of taste cells. Boeke ('17), Olmstead ('20), and May ('25) found that it is the regenerating sensory nerves which bring about the formation of the new taste cells, following experimental degeneration of the taste buds.

All of these observations may be indicative of the presence of some stimulating substance (secretion) given off by the regenerating nerve which activates the formation of a new taste bud, and it may be that the sensory hyperplasias which have been related to the influence of in-

growing neurones, may be brought about in the same way.

How far hormone action or some allied activity is effectual in these processes it is, of course, difficult to determine.

SELECTIVITY OF NEURONES

Observations by Kappers ('17, '21, '22), Child ('21), Bok ('15), Ingvar ('20) and others offer grounds for theories of the

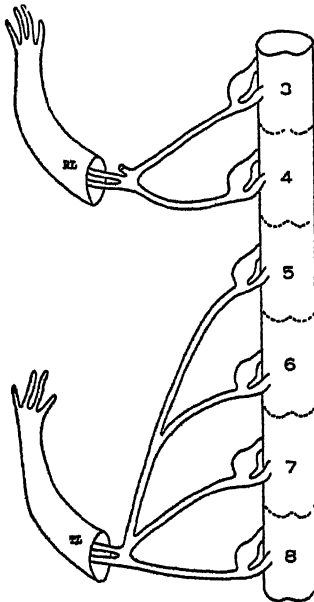


FIG. 10. A DIAGRAMMATIC PLAN OF THE SEGMENTAL NERVE CONTRIBUTION TO THE TRANSPLANTED LIMB (TL) AND THE REGENERATED LIMB (RL) IN CASE AS₄₁₃

Right anterior limb grafted to position four body segments caudal to the normal. Regeneration of limb in orthotopic position. The normal brachial nerves arise from the third, fourth, and fifth segments of the cord.

development of neurone pattern and selectivity within the nervous system on the basis of bioelectric potentials within the organism, yet when we consider the question of cellular proliferation, peripheral selectivity of axones and other allied phenomena, many interpretations seem

difficult unless it is assumed that more or less specific substances (hormones) which exert an attractive influence, are at work. Child ('21) in his discussion of neurone pattern says that in the connection of the nerves with the peripheral territory, chemotaxis may play a part. Herrick ('25) also considers this a real factor in nervous differentiation although he points out that this action is not very specific as is readily indicated by the fact that nerves will grow and effect functional connections in most atypical places. In this connection he cites Burr's ('20) experiments on transplanted olfactory placodes, Stone's ('24) experiments on the transplantation of other cranial placodes, and my own observations on the spinal nerves of *Amblystoma* in effecting connections with transplanted limbs. In the limb experiments it was found that brachial nerves of *Amblystoma* larvae would grow considerable distances out of their normal course to effect functional connection with the grafted appendage ('20b, '22), yet when the limb was grafted at too great a distance, spinal nerves which normally never enter a limb, produced the brachial plexus, in spite of the so-called "preference" of the brachial nerves for their own end-organ. In none of the limb experiments has there ever been any evidence of an absolute muscle-neurone specificity. The same is brought out in the experiments of Harrison ('07a), Braus ('05) and also more recently by Weiss ('23b).

In some recent limb experiments (Detwiler, '25b) the right anterior limb of *Amblystoma* was transplanted the distance of four body segments caudal to the normal situation, under conditions allowing for the regeneration of an appendage in the normal position (figs. 16, 17). This procedure was adopted with the view of bringing about limb development in both heterotopic and orthotopic posi-

tions, and in such a way that initial limb development in the heterotopic position might be advanced over that in the orthotopic position. In many such cases with two anterior limbs, the normal brachial nerves (third, fourth and fifth) were distributed to both appendages although such distribution did not always involve any peripheral communication of the nerves (fig. 10). In several cases, the fifth nerve, which typically supplies the normal limb, was found to grow caudally a considerable distance and supply a large portion of the musculature of the grafted limb. Weiss ('23a, '23b, '23c, '24) recently reported interesting grafting experiments upon differentiated limbs of salamander larvae. In cases where a forelimb was placed near an intact hind limb, the hind limb nerves which were severed in the operation became redistributed to both limbs. In one such case complete innervation of the grafted limb originated from branches of the third lumbar nerve, which normally innervates only the adductors of the femur and the flexors of the knee. Analogous movements of the homologous muscles which were observed in both the experiments of Weiss and myself cannot be correlated, therefore, with specific nerve regeneration to homologous muscles. The acquisition of nerves by the grafted limbs in both types of experiments tends to point towards a similarity between the attractive influence exerted by degenerating nervous tissue in the regenerating nerves such as Weiss observed, and that exerted by the differentiating limb rudiment on outgrowing nerves as was found in my own experiments. It is obvious from the latter experiments that the transplanted limb exerts a stronger influence on the fifth nerve (caudal of the brachial nerves) than does the regenerating limb, otherwise the fifth nerve should supply the orthotopic

extremity just as it does under normal conditions. When the normal limb rudiment is not removed and an additional limb rudiment is placed three or four segments caudal to it, the latter is never supplied by the fifth nerve.

It is difficult to analyze the exact nature of this attraction. The differentiating limb rudiment must be regarded as a region of high physiological activity. According to Child ('21) such regions are electropositive with respect to their surroundings. Such being the case, it is conceivable that the axones coming into the general vicinity of the differentiating limb are attracted by the electric field, and electrical polarization may be brought about much after the same fashion as obtains in the central nervous system according to Kappers ('17, '21) or Child ('21). This seems to be applicable to any nerve which develops in the vicinity of the electric field. It may be exemplified by the fact that limbs placed in a position four segments caudal to the normal may receive nerves from the fourth to the eighth segments inclusive, but "preference" seems to be given to the fifth and sixth, presumably because the outgrowth of the nerves from these levels of the cord are in advance of those caudal to them. The only reason offered in explanation of the failure of the third and fourth nerves to grow caudally to the transplanted limb is because the point of high physiological activity (differentiating transplanted limb rudiment) is too far removed to be effective on such a cephalic level.

In the cases with a heterotopic limb placed four segments caudal to the normal and a regenerating limb in the orthotopic position, we have two centers of high physiological activity, but the growth activity of the grafted limb rudiment is exerted earlier than that of the regenerat-

ing one by reason of the initial delay resulting from reorganization in the latter.

Kappers ('21) suggests the probability that in embryos, the proliferation of muscle has the same influence as functioning adult tissue, and that this proliferating tissue may thus activate irradiations of nervous currents from the spinal cord. He makes use of the observations of Herrick and Coghill ('15) on the development of reflex mechanisms in *Amblystoma*, and suggests that the initial contraction of the myotomes sets free action currents already present in the longitudinal tracts of the central nervous system, as was evidenced by the fact that the primary root fibers originate as collaterals from these longitudinal tracts. (Herrick and Coghill, op. cit., fig. 3.)

Bok ('17) has pointed out that the connection between certain muscles and sometimes widely distant places of the central nervous system has to be explained by the fact that the contraction of muscle (which precedes the formation of nerve roots) exerts a trophic action upon the central fibers.

Further evidence of the attraction of differentiating muscle on nerve is shown by the experiments of Hoadley ('25), who transplanted pieces of embryonic chick mesencephalon and somitic tissue to the chorio-allantoic membrane. He found that the nerve fibers which normally are never related to muscle (visual correlation fibers) will grow out from the mesencephalon into the differentiating muscle.

Since these fibers will also penetrate into other tissues, Hoadley says that the attraction must be of a very general nature, and in his analysis of the situation is inclined to view the attraction as a dynamic process (galvanic) rather than one of chemotaxis.

Although bio-electric conditions may be responsible for the general ingrowth of axones into a field of rapid proliferation by reason of the high physiological activity set up—hence an electrical polarization (Child, '21), it does not appear to the writer that in the present state of our knowledge we can account for the peripheral selectivity of nerve with muscle without assuming that the muscle or groups of muscle produce substances (hormones?) at particular periods of their differentiation, which act chemotactically upon nerve fibers which are growing into their general vicinity.

In our eye transplantation experiments (May and Detwiler, '25) we found that, in general, there was a shifting of the ganglion towards the entering optic nerve from the transplanted eye. In one case where the transplanted optic nerve entered the medulla, there was a shifting of the nerve cells from their normal position into the white matter at the point of entrance of the nerve. We have already discussed this reaction and similar ones in the light of the theory of neurotropism of Cajal, and of Kappers' neurobiotaxis theory. We also raised the question as to whether or not the cell migration towards

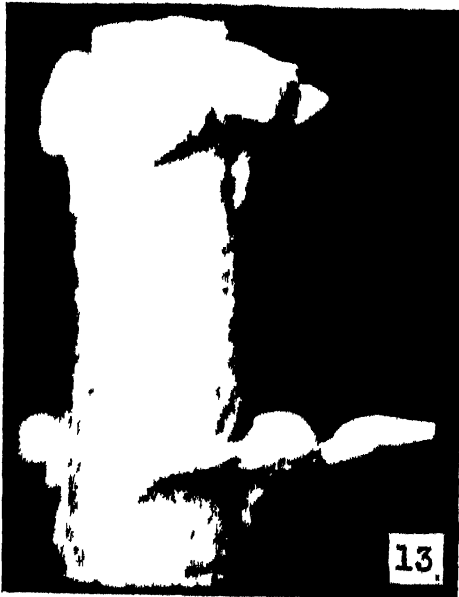
PLATE 1

FIG. 11. Photograph of reconstruction models of the left third and fourth spinal ganglia which are in connection with the normal intact anterior limb. $\times 50$. Case AS₄₈.

FIG. 12. Photograph of reconstruction models of the right third and fourth spinal ganglia, showing reduction in size resulting from excision of the limb with which they are normally connected. $\times 50$.

FIG. 13. Photograph of reconstruction models of the normal left sixth and seventh spinal ganglia which normally have no connection with a limb. $\times 50$.

FIG. 14. Photograph of reconstruction models of enlarged right sixth and seventh spinal ganglia supplying afferent nerves to a transplanted limb. $\times 50$.



the entering optic nerve might be an ontogenetic example of Kappers' phylogenetic theory. Further experiments along this line are in progress.

REGENERATION

The agencies which are operative in reparation of the central nervous system of amphibian larvae following experimental injury have been studied in an experimental way by a number of investigators. Hooker ('15) completely severed the spinal cord of frog embryos at the stage of closed neural folds with a view of analyzing the processes leading to its reunion. He found that the spinal cord underwent complete regeneration and that the process of reunion is affected primarily by the development of nerve fibers which bridge the gap and establish physiological continuity. He calls attention to similar observations made by Brown-Séquard ('49) and by Harrison ('10b). Whereas Hooker found that both pieces of the sectioned cord played a rôle in the reunion process, Masius and Van Lair ('69) claimed that the caudal stump played no part in the regeneration of the cord in adult frogs.

Hooker (*op. cit.*) found that when the cut ends of the spinal cord were brought into contact with each other, healing per primam resulted. When the wound surfaces were somewhat separated, reunion was established by a definite sequence of events. Using his wording these are: (a) the development of nerve fibers from the motor cells of each segment of the cord, (b) the growth of sensory axones from the cut surface of the posterior stump, (c) the outgrowth of fibers from the epithelial cells of the *canalis centralis* of either end of the cord, (d) the wandering of neuroblasts into the fibrous net between the cut ends from both stumps, and (e) the elongation of both ends of the spinal cord to-

wards each other by the proliferation of epithelial cells of the *canalis centralis* and the consequent lengthening of the canal.

Hooker also showed that the elements entering into the regenerated portion of the cord are derived entirely from the original cord, and that neither connective tissue nor epithelium take any part in the process.

In his second paper, Hooker ('17) reports the results of reversing end-for-end a portion of the cord on the healing of the cord wounds, the polarity of the elements of the cord, and upon the behavior of the larvae. He found as did Spemann ('12) that the reversed piece retained its original anatomical polarity. Under simple section of the cord the reunion is established first by the caudal growth of the motor processes from the cephalic stump, which in turn is followed by the cephalic growth of sensory processes. In the embryo with a reversed middle piece, following double section of the cord in the cervical region, the normal relationship between the direction of the growth of all the processes and the antero-posterior axis of the body has been completely upset so that the nerves which were originally descending processes grew in an ascending direction and vice versa. Also the reversal brings together at the cephalic wound surface a series of nerve fibers growing in the opposite direction which are all descending processes, and, at the caudal wound a number of fibers growing in both directions which are ascending processes. Under these conditions there was present a marked tendency on the part of the nerve fibers to avoid entering the opposite wound surface. In spite of this "antagonism" between "like" surfaces, fibers did bridge the gap in many cases and re-establish continuity.

Although the neurones begin their

development in the normal orientation to the reversed piece, the direction of the transmission of stimuli is reversed as evidenced by the normal reflex behavior of the larvae. Regarding this point Hooker (op. cit., page 445) remarks

. . . . It is of course doubtful whether there is any real specificity of ascending and descending processes and the physiological results obtained certainly demonstrate that a considerable degree of adaptation has taken place here, in that the descending processes must certainly function as ascending processes and vice versa. In this sense, therefore, we must conclude that there is a reversal in the polarity of the elements contained within the reversed piece of the spinal cord, though whether this reversal in polarity includes anatomical reversal of the cells themselves is very doubtful. It is much more probable that only the direction in which the stimuli travel along the processes is the reverse of its usual course.

Corroboration of such functional reversal as obtained by Hooker has been physiologically brought out in the spinal cord reversal experiments in *Amblystoma* embryos (Detwiler, '23b).

In a recent paper Hooker ('25) has described the processes which establish anatomical continuity in transected cords of frog tadpoles, and his paper gives a résumé of work done by other investigators in this field. His observations show

that the structural restoration of the severed spinal cord demands the presence of four types of elements. According to him these are: ependymal cells, neuraxes derived from neuroblasts of the original cord, spongioblasts, and neuroblasts. The principal problem according to him is the supply of spongioblasts and neuroblasts to restore the other elements of the cord. Apparently the necessary neuroblasts and spongioblasts may be derived by the cytomorphosis of cells already present, or by the production of additional elements by proliferation. A shifting of cells and their migration for greater or lesser distances also seems to be necessary.

In addition to showing the cellular elements requisite for regeneration of the cord, and the methods by which the repair processes are carried out, Hooker's ('25) observations also indicate the existence of some directive stimulus on the growth of the neuraxes. The same conclusion is made by de N6 ('21) who speaks of it as a neurotropism.

Other evidence of attraction in the growth and restitution processes following cord transection are brought out in the experiments of Wieman ('22). Wieman rotated pieces of spinal cord at ninety degrees to the antero-posterior axis and

PLATE 2

FIG. 15. Photograph of *Amblystoma* larva showing right anterior limb transplanted the distance of four body segments caudal to the normal position. Fifty days after operation. $\times 2$.

FIG. 16. Photograph of *Amblystoma* larva (fifty-three days after operation), showing right anterior limb transplanted (with inverted orientation) the distance of four body segments caudal to the normal position. Regeneration of limb in orthotopic position. $\times 2$.

FIG. 17. Photograph of *Amblystoma* larva (fifty days after operation) with right anterior limb rudiment transplanted the distance of three body segments caudal to the normal position. Transplanted extremity completely reduplicated. Regeneration of limb in orthotopic position. $\times 2$.

FIG. 18. Photograph of *Amblystoma* larva (seventy days after operation) in which the anterior limb region of the spinal cord (third, fourth, and fifth segments) was excised and replaced by a more caudal unit of cord (seventh, eighth and ninth segments) from another embryo. $\times 2.2$.

FIG. 19. Photograph of *Amblystoma* larva showing transplanted eye in position of the ear. $\times 4$.

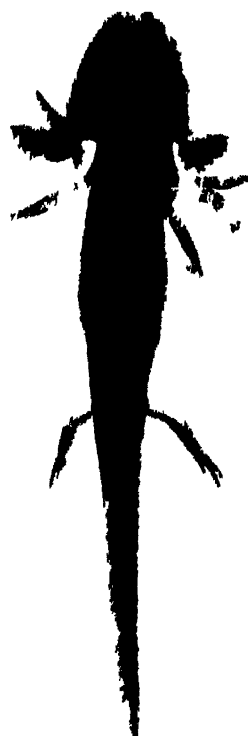
FIG. 20. Photograph of *Amblystoma* larva TrSc 30 in which the third, fourth, and fifth spinal segments have been replaced by a unit of cord comprising the first, second and third segments from another embryo. $\times 2.4$.



15



16



18



19



purposefully interposed somitic tissue between the intact stumps and the rotated piece. In this way healing per primam was prevented, and the reunion was established first by the caudal growth of descending processes which was followed by the cephalic growth of ascending processes as observed by Hooker ('17). He found that the descending processes always pierce the rotated piece through its originally cephalic end, and the ascending ones always enter the originally caudal surface, yet the chances for the opposite course are equally advantageous as far as distance is concerned. Wieman corroborates Hooker in that the descending tracts are reestablished before the ascending ones. In fact Wieman states that the development of ascending tracts depends upon a prior formation of descending ones through the operated region. This is strongly suggested by the greater frequency of fusion between the rotated piece and the stump found to obtain in higher levels of the cord as compared with the more caudal levels. The relation found to occur between the time of motor and sensory reunion bear out in an experimental way Coghill's observations on the development of reflex arcs of the cord.

Wieman ('25) found, that when the sectioned piece was oriented at 135 degrees to the normal, some cases healed per primam and a complete reversal of functional polarity ensued. In others, the isolation of the transplanted piece was maintained for a long enough time to allow the inherent polarity to come to full expression. In such cases descending connections failed. Wieman believes that this is due to the fact that the metabolic gradient set up at an angle of 135 degrees to the principal gradient inhibits the formation of descending tracts to a greater extent than when the gradient of the transplanted piece forms an angle of 90 degrees.

Wieman's results show that nervous reunion between the transplanted neural tube and stumps depends primarily upon the development of descending outgrowths from the anterior neural stump.

Since both Hooker and Wieman find that the first repair process in cases not healing per primam is the outgrowth of neuraxes, and that this is followed by proliferation of cells in the original cord (Hooker, '25), it may be that this proliferation is set up under a stimulative influence of fiber invasion. If this should actually prove to be the case, it would place regeneration processes at least in part upon the same basis as those found in normal morphogenesis.

Another subject of general interest to the students of the nervous system pertains to the influence of the developing nervous system upon the morphogenesis and regeneration in other systems. This matter is under experimental investigation and constitutes a subject which space will not permit of discussion in this paper. Recent researches by Weiss ('25) and by Hamburger ('25) show a controlling influence of the nervous system upon the normal development and regeneration of the extremities in amphibians. Their papers contain discussions of the researches of others in this field, as well as valuable bibliographies.

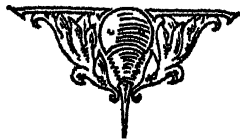
It has not been the purpose in this communication to review the entire subject of morphogenesis in the nervous system, but merely to point out the trend of certain lines of experimentation in this field, and the results which they have so far achieved. It is hoped that continued work along such and other lines may contribute to clearer interpretations of the perplexing problems of morphogenesis and to our knowledge of structure-function correlations in the nervous system.

LITERATURE LIST

- BANCHI, H. 1906. Sullo sviluppo bei nervi periferici in maniera indipendente dal sistema nervosa centrale. *Anat. Anz.*, Bd. 28.
- BELLAMY, A. W. 1919. Differential susceptibility as a basis for modification and control of early development in the frog. *Biol. Bull.*, vol. 37.
- BOEKE, J. 1917. Studien zur Nervenregeneration. II. Die Regeneration nach Vereinigung ungleichartigen Nervenstücke (heterogene Regeneration) und die Funktion der Augenmuskel- und Zungenerven. Die allgemeinen Gesetze der Nervenregeneration. *Verhand. d. Koninkl. Akad. v. Wetensch.* t Amsterdam, D. 19.
- BOX, S. T. 1915. Die Entwicklung der Hirnnerven und ihrer zentralen Bahnen. Die stimulogene Fibrillation. *Folia Neurobiolog.*, Bd. 9.
1917. The development of reflexes and reflex tracts. 1. The reflex circle. *Psychiat. en Neurolog.* Bladen, Amsterdam, vol. 21.
- BRAUS, H. 1904. Einige Ergebnisse der Transplantation von Organanlagen bei *Bombinator* larven. *Verh. Anat. Ges.*, Bd. 28. Vers. Jena.
1905. Experimentelle Beiträge zur Frage nach der Entwicklung peripherer Nerven. *Anat. Anz.* Bd. 26.
1906. Vordere Extremität und Operculum bei *Bombinator* larven. *Morph. Jahr.*, Bd. 35.
- BROWN-SQUARD, C. E. 1849. Exposé sur la curabilité des plaies de la moelle épinière. *Compt. rend. Soc. Biol.*, T. 1.
- BURR, H. S. 1916a. The effect of the removal of the nasal placodes on *Amblystoma* embryos. *Jour. Exp. Zool.*, vol. 20.
- 1916b. Regeneration in the brain of *Amblystoma*. *Jour. Comp. Neur.*, vol. 26.
1920. The transplantation of the cerebral hemispheres of *Amblystoma*. *Jour. Exp. Zool.*, vol. 30.
1923. Experimental hyperplasia of the cerebral hemispheres in *Amblystoma*. *Anat. Rec.*, vol. 25.
- BURROWS, M. T. 1911. The growth of tissues of the chick embryo outside the animal body with special reference to the nervous system. *Jour. Exp. Zool.*, vol. 10.
- CAJAL, S. RAMÓN Y. 1890. A quelle époque apparaissent les expansions des cellules nerveuses de la moelle épinière des poulets. *Anat. Anz.*, Bd. 5.
1892. La rétine des vertébrés. *La Cellule.* T. 9.
1894. Les nouvelles idées sur la structure du système nerveux chez l'homme et chez les vertébrés. Paris.
1906. Genesis de las fibras nerviosas del embrión y observaciones contrarias a la teoría catenaria. *Trab. Lab. Invest. Biol. Univ. Madrid*, T. 4.
- CHILD, C. M. 1921. The Origin and Development of the Nervous System. Univ. Chicago Press. Chicago.
1924. Physiological Foundations of Animal Behavior. Henry Holt and Co., New York.
- COOCHILL, G. E. 1923. The growth of neuroblasts in relation to physiological and differential rates of metabolism. Abstracts of papers, Amer. Assoc. Anatomists, Chicago.
- 1924a. Correlated anatomical and physiological studies of the growth of the nervous system in Amphibia. III. The floor plate of *Amblystoma*. *Jour. Comp. Neur.*, vol. 37.
- 1924b. Correlated anatomical and physiological studies of the growth of the nervous system in Amphibia. IV. Rates of proliferation and differentiation in the central nervous system of *Amblystoma*. *Jour. Comp. Neur.*, vol. 37.
- DETWILER, S. R. 1920a. On the hyperplasia of nerve centers resulting from excessive peripheral loading. *Proc. Nat. Acad. Sci.*, vol. 6.
- 1920b. Experiments on the transplantation of limbs in *Amblystoma*. The formation of nerve plexuses and the function of the limbs. *Jour. Exp. Zool.*, vol. 31.
1922. Experiments on the transplantation of limbs in *Amblystoma*. Further observations on peripheral nerve connections. *Jour. Exp. Zool.*, vol. 35.
- 1923a. Experiments on the transplantation of the spinal cord in *Amblystoma* and their bearing upon the stimuli involved in the differentiation of nerve cells. *Jour. Exp. Zool.*, vol. 37.
- 1923b. Experiments on the reversal of the spinal cord in *Amblystoma* embryos at the level of the anterior limb. *Jour. Exp. Zool.*, vol. 38.
1924. Further observations on proliferation of nerve cells in grafted units of spinal cord. *Anat. Record*, vol. 27.
- 1925a. The results of substituting an extraneous medulla for the cephalic end of the embryonic spinal cord in *Amblystoma*. *Jour. Exp. Zool.*, vol. 41.
- 1925b. Coordinated movements in supernumerary transplanted limbs. *Jour. Comp. Neur.*, vol. 38.
- 1925c. Spinal cord injury and nerve cell proliferation in the embryo. *Anat. Record*, vol. 30, 39.
- 1925d. An experimental study of cellular proliferation in the anterior end of the spinal cord of *Amblystoma*. *Jour. Exp. Zool.*, vol. 42.

- DETWILER, S. R., AND LEWIS, RUTH. 1925. Size changes in primary brachial motor neurones following limb excision in *Amblystoma*. Jour. Comp. Neur., vol. 39.
- DE NÓ, R. LORENTE. 1921. La regeneración de la medula espinal en las larvas de batracio. Trabajos. T. 19.
- DÜRKERN, B. 1911. Über frühzeitige Extirpation von Extremitätenanlagen beim Frosch. Zeit. f. wiss. Zool., Bd. 99.
- FORREL, AUGUST. 1887. Einige hirnanatomische Betrachtungen und Ergebnisse. Arch. für Psychiatrie. Bd. 18.
- GEMELLI, F. A. 1906. Ricerche sperimentali sullo sviluppo dei nervi degli arti pelvici di *Bufo vulgaris* innestati in sede anomala. Rivista di Pathologia Nervosa e Mentale. Anno. 11.
- HAMBURGER, VICTOR. 1925. Über den Einfluss des Nervensystems auf die Entwicklung der Extremitäten von *Rana fusca*. Arch. f. mikros. Anat. u. Entw.-mech., Bd. 105.
- HARRISON, R. G. 1904a. Neue Versuche und Beobachtungen über die Entwicklung der peripheren Nerven der Wirbeltiere. Sitz.-Ber. Niederrh. Ges. Natur. u. Heilkunde. Bonn.
- 1904b. An experimental study of the relations of the nervous system to the developing musculature in the embryo of the frog. Am. Jour. Anat., vol. 3.
1906. Further experiments on the development of peripheral nerves. Amer. Jour. Anat., vol. 5.
- 1907a. Experiments in transplanting limbs and their bearing upon the problems of the development of nerves. Jour. Exp. Zool., vol. 4.
- 1907b. Observations on the living developing nerve fiber. Anat. Record, vol. 1.
- 1910a. The outgrowth of the nerve fiber as a mode of protoplasmic movement. Jour. Exp. Zool., vol. 9.
- 1910b. The development of peripheral nerves in altered surroundings. Arch. f. Entw.-mech., Bd. 30.
- HENSEN, V. 1864. Über die Entwicklung des Gewebes und der Nerven im Schwanz der Froschlärve. Virchow's Archiv. Bd. 31.
- HERRICK, C. J. 1914. The medulla oblongata of larval *Amblystoma*. Jour. Comp. Neur., vol. 24.
1922. Some factors in the development of the Amphibian nervous system. Anat. Rec., vol. 23.
1925. Morphogenetic factors in the differentiation of the nervous system. Physiol. Reviews, vol. 5.
- HERRICK, C. J., AND COOHILL, G. E. 1915. The development of reflex mechanisms in *Amblystoma* embryos. Jour. Comp. Neur., vol. 25.
- HIS, W. 1886. Zur Geschichte des menschlichen Rückenmarks und der Nervenwurzeln. Abh. d. math.-phys. Kl. d. Kgl. Sachs. Ges. d. wiss., Bd. 13.
1887. Die Entwicklung der ersten Nervenbahnen beim menschlichen Embryo. Arch. f. Anat. u. Physiol. Anat. Abt.
1888. Zur Geschichte des Gehirns sowie der centralen und peripherischen Nervenbahnen beim menschlichen Embryo. Abh. d. math.-phys. Kl. d. Kgl. Sachs. Ges. d. wiss., Bd. 14.
1890. Histogenese und Zusammenhang der Nervelemente. Arch. f. Anat. u. Phys., Anat. Abt. Suppl. Bd.
- HODLEY, LEIGH. 1925. The differentiation of the isolated chick primordia in chorio-allantoic grafts. III. On the specificity of nerve processes arising from the mesencephalon in grafts. Jour. Exp. Zool., vol. 42.
- HOOKE, DAVENPORT. 1915. Studies on regeneration in the spinal cord. I. An analysis of the processes leading to its reunion after it has been completely severed in frog embryos at the stage of closed neural folds. Jour. Comp. Neur., vol. 25.
1917. Studies on regeneration in the spinal cord. The effect of reversal of a portion of spinal cord at the stage of closed neural folds on the healing of the cord wounds, on the polarity of the elements of the cord and on the behavior of frog embryos. Jour. Comp. Neur., vol. 27.
1923. The nature of the division of neuroblastic cells in the regenerating spinal cords of Amphibian larvae. Anat. Rec., vol. 24.
1925. Studies on regeneration in the spinal cord. III. Reestablishment of anatomical and physiological continuity after transection in frog tadpoles. Jour. Comp. Neur., vol. 38.
- INGVAR, SVEN. 1920. Reaction of cells to the galvanic current in tissue cultures. Proc. Soc. Exp. Biol. and Med., vol. 17.
- KAPPERS, C. U. ARIËNS. 1917. Further contributions on neurobiotaxis. IX. An attempt to compare the phenomenon of neurobiotaxis with other phenomena of taxis and tropism. The dynamic polarization of the neurone. Jour. Comp. Neur., vol. 27.
1921. On structural laws in the nervous system: The principles of neurobiotaxis. Brain, vol. 44.
1922. Dixième contribution à la théorie de la neurobiotaxis. L'Encephale, i, 1.
- LANDAUER, F. L. 1907. On the place of the origin and method of distribution of taste buds in *Amiurus melas*. Jour. Comp. Neur., vol. 17.
- V. LENTHOSSÉ, M. 1892. Beobachtungen an den Spinalganglien und dem Rückenmark von *Pseudosinus* embryonen. Anat. Anz., Bd. 7.

- V. LENHOSSEK, M. 1895. Der feinere Bau des Nervensystems im Lichte neuester Forschungen. Berlin.
1906. Zur Frage nach der Entwicklung der peripheren Nervenfasern. *Anat. Anz.*, Bd. 28.
- LEWIS, M. R., AND W. H. 1911. The cultivation of tissues from chick embryos in solutions of NaCl, CaCl₂, KCl, NaHCO₃. *Anat. Rec.*, vol. 5.
- MARCHAND, L. 1902. Développement des papilles gustatives chez le foetus humain. *Compt. Rend. Soc. Biol. Paris*, T. 54.
- MASTUS, V., UND VAN LAIR, C. 1869. Anatomische und funktionelle Wiederherstellung des Rückenmarks beim Frosch. (Vorläufige Mittheilung). *Centrbl. f. d. med. Wissen.*, 7.
- MAY, R. M. 1925. The relation of nerves to degenerating and regenerating taste buds. *Jour. Exp. Zool.*, vol. 42.
- MAY, R. M., AND DETWILER, S. R. 1925. The relation of transplanted eyes to developing nerve centers. *Jour. Exp. Zool.*, vol. 43.
- OLMSTEAD, J. M. D. 1920. The nerve as a formative influence in the development of taste buds. *Jour. Comp. Neur.*, vol. 31.
- ROUX, W. 1885. Einleitung. *Archiv. f. Entw.-mech. des Organismen*, Bd. 1.
- SHORRY, M. L. 1909. The effect of the destruction of peripheral areas on the differentiation of neuroblasts. *Jour. Exp. Zool.*, vol. 7.
1911. A study of the differentiation of neuroblasts in artificial culture media. *Jour. Exp. Zool.*, vol. 10.
- STONE, L. S. 1924. Experiments on the transplantation of placodes of the cranial ganglia in the amphibian embryo. I. Heterotopic transplantations of the ophthalmic placode upon the head of *Amblystoma punctatum*. *Jour. Comp. Neur.*, vol. 38.
- SPEHMANN, H. 1912. Über die Entwicklung ungedrehter Hirnteile bei Amphibienembryonen. *Zool., Jahrb., Suppl. Bd.* 15.
- SZYMONOWICZ, W. L. 1895. Beiträge zur Kenntniss der Nervenendigungen in Hautgebilden. *Arch. f. mikros. Anat.*, Bd. 45.
1896. Ueber den Bau die Entwicklung der Nervenendigungen im Entenschnabel. *Arch. f. mikros. Anat.*, Bd. 48.
- WEISS, PAUL 1923a. Die Funktion transplantierter Amphibien-extremitäten. II. Kompensatorische Reflexe. *Sitzungsber. d. Akad. d. Wiss. Wien. Akad. Anz.*, Nr. 10, Mitt. 99.
- 1923b. Die Funktion transplantierter Amphibienextremitäten. III. Histologische Untersuchungen über die Nervenversorgung der Transplantate. *Sitzungsber. d. Akad. d. Wiss. Wien. Akad. Anz.*, Nr. 22-23, Mitt. 80.
- 1923c. Die Funktion transplantierter Amphibienextremitäten. IV. Theorie: Die Erfolgsorgane als Resonatorensystem. *Ibid.*, Mitt. 101.
1924. Die Funktion transplantierten Amphibienextremitäten. Aufstellung einer Resonanztheorie der motorischen Nerventätigkeit auf Grund abgestimmter Endorgane. *Archiv. für mikros. Anat. u. Entw.-Mech.*, Bd. 102.
1925. Abhängigkeit der Regeneration entwickelter Amphibienextremitäten vom Nervensystem. *Archiv. f. mikros. Anat. u. Entw.-Mech.*, Bd. 104.
- WIERMAN, H. L. 1922. The effect of transplanting a portion of the neural tube of *Amblystoma* to a position at right angles to the normal. *Jour. Exp. Zool.*, vol. 35.
1925. Further observations on the angular transplantations of the neural tube of *Amblystoma*. *Jour. Exp. Zool.*, vol. 41.





A REVIEW OF THE DISCOVERY OF PHOTOPERIODISM: THE INFLUENCE OF THE LENGTH OF DAILY LIGHT PERIODS UPON THE GROWTH OF PLANTS

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LIGHT is so obviously important for the well-being of most living things that, as might be expected, there is a wealth of literature describing the results of careful studies of the effect on plants of sunlight and of artificial light, of light of different colors, and of different intensities.

It was not, however, until the painstaking and brilliant researches of Dr. W. W. Garner and his associates that the remarkable significance of changes in the duration of the daily periods of light and darkness was realized. For many plants, perhaps for most plants of the temperate zone, the length of the day—that is, the number of hours and minutes of continuous daylight—is a far more critical factor in determining character of growth than is the intensity of the light. For example, the common blue violet is known as a typical spring flower. In other words, these blue flowers are produced at a time of year when the daylight period is relatively short. Violets may be produced at any season of the year, however, by exposing the plants to the proper number of hours of light (plate 1, A); thus even in midsummer typical blue violets may be secured by placing the plants in an absolutely dark room, and each day bringing them out into the sunlight for a period of about 10 hours. On the other hand, the common rosemallow does not

flower unless it is exposed daily to a light period of more than 12 hours. Buckwheat, which is capable of producing flowers throughout the range of a daylight period varying from 5 hours up to 20 hours, and probably even in continuous illumination, is an extreme example of a third type of plants, overlapping but very distinct from the first two.

PHOTOPERIODISM

Garner has coined the word "photoperiodism" to designate these responses to length of day, and for convenience in describing the behavior of different plants has arbitrarily grouped those experimented with up to the present time into (1) short-day, (2) long-day, and (3) ever-blooming plants.

Using the equatorial length of day of 12 hours as a standard, plants belonging to the first or short-day group are those which can bloom only under a daily light period of 12 hours or less; plants of the second or long-day group can bloom only in a day light length of more than 12 hours; plants of the third group are capable of blooming throughout these ranges. It should be noted that not only botanical species but even horticultural varieties and strains differ markedly as to the particular length of day most favorable for flowering. Furthermore, they also differ widely as to the narrowness of the range

in day length which will permit flowering. Climbing hemp-weed, for example, can flower only between the daylight ranges of $13\frac{1}{2}$ hours to $15\frac{1}{2}$ hours, the most favorable period being approximately between these figures. The Biloxi variety of soybeans, however, which cannot flower in a day length in excess of 13 hours and with an optimum flowering period of approximately 10 hours, cannot be given a sufficiently short light day to entirely suppress flowering and maturity. The continuity of the light period has been assumed in these statements. Alternate exposure to 1-hour periods of light and darkness, although perhaps enabling a plant to grow vigorously, is not equivalent to a 12-hour daily exposure to continuous light; and plants which normally flower actively in the 12-hour daylight period are totally unable to flower under alternate hours of light and darkness, even though they are thus receiving 12 hours of light out of the 24. Curiously enough, however, a single break in an extended daylight period appears to have little if any effect upon the response to the light period measuring from the beginning to the end. A plant, such as the Biloxi soybean (plate 1, B), capable of flowering actively in a 12-hour light period will continue to develop in an apparently identical manner if placed in the dark during 2 hours in the center of each light period so that it is actually receiving but 10 hours of light daily instead of 12. It would thus seem that whatever reactions or processes may be initiated in the plant by the light rays, some time is required to bring about these responses, and that the momentum of the reaction is sufficient to bridge the gap caused by a single short dark period in the middle of the day. It is not possible, as yet, to determine how extensively the light period may be broken before interfering

with its controlling effect on the plant; nor is it possible to determine the limits of decreasing intensity of light below which plants do not react. It is noteworthy, however, that supplementing the daily period of sunlight with ordinary incandescent lights of approximately one one-thousandth of the intensity of sunlight is sufficient to bring about the flowering response of long-day plants.

LENGTHENING DAYS WITH ELECTRIC LIGHT

Equipping an ordinary greenhouse with incandescent lights giving an average light intensity of about 4 candlepower at the surface of the soil was found sufficient for bringing many plants into blossom, although this light contains practically no ultra violet rays and is equally lacking in many other rays present in sunlight. Even differences in color of light have been found of relatively little significance in causing or preventing flowering. This weak light used to supplement the short days of the winter season was turned on at sunset and extinguished at midnight in each 24 hours. The short-day plants, such as common cosmos and narrow leaved sunflower (plate 2, A and B) in the artificially-lighted greenhouse were unable to flower but continued vigorous vegetative growth. When grown in a greenhouse receiving only the natural light of the winter day but under the same conditions of temperature and moisture these same species of plants, though very small, flowered promptly. The long-day plants, on the other hand, such as golden rod and Coreopsis (plate 3, A and B) grew but poorly in the greenhouse receiving only winter daylight, while they grew vigorously and produced their flowers in a normal summer manner in the greenhouse where the winter day was artificially lengthened by the electric light. Spinach planted in the naturally lighted greenhouse developed a

typical rosette of leaves throughout the winter, while in the electrically-lighted house it bloomed within 6 weeks of germination. Spinach is mentioned particularly, because hitherto the generally accepted idea of the outgrowing of the rosette stage and sending up blooming stalks of spinach is that it was caused by the advancing temperature of summer.

LOCALIZED FLOWERING RESPONSE

The extremely local character of the flowering response to the daylight period is so remarkable that it deserves special consideration. Using cosmos as the basis of the experiment, young seedlings propagated under long-day conditions were cut back and forced to develop two approximately equal branches. Some time afterward cardboard screens were placed between the two branches so that each branch of the same plant could be given different periods of illumination (plate 4, A). Under these conditions the branch exposed to the short day promptly flowered, matured, and passed into a typical state of decline following maturity, while the branch exposed to the longer illumination period continued the vigorous vegetative type of growth. The lower stem of the plant continued to grow in harmony with the development of the vegetative branch and apparently was unaffected by the mature and dying condition of the branch which had fruited. Elaborating these experiments, specially constructed light-proof boxes were placed about different portions of a well developed cosmos plant. When the upper portion of the plant was exposed to approximately 15 hours of light while the lower portion was given 10 hours of light, flowers promptly developed on the lower portion, while the upper portion remained in vigorous vegetative condition. When both the top and bottom third of the

plant were exposed to the short light period and the central portion was exposed to the longer light period, flowering and fruiting on the top and bottom thirds very soon developed while the central portion remained vigorously vegetative (plate 4, B). If carefully handled, these localized responses may be continued for several months. In so far as the development of the flowering habit is concerned, therefore, it seems that each portion of the plant is capable of responding to the stimulus of the light period in much the same manner as if it were a separate plant.

LIGHT AS AN ECOLOGICAL FACTOR

The daylight period exerts a very striking and determinative influence on many phases of growth as well as upon flowering and fruiting but before discussing these more involved problems especial attention should be called to the important action of the light period in differentiating groups of plants by its limiting effect upon their ability to reproduce their species. Other environmental factors, such as temperature, moisture, and character of food supply also exert a selective action, but usually each of these factors may change throughout a rather wide range before the existence of the individual plant is jeopardized or its behavior or type of growth (as distinguished from vigor of growth) is markedly affected. The light period, however, exhibits a diversity of effect upon different kinds of plants of a more far-reaching character. Plants which require a long day to flower and fruit obviously can not maintain themselves in the tropical zone, where the day remains about 12 hours for the entire year, even though high altitude may hold the temperature well below the danger limit for the species. The more extreme type of short-day plants are, of course, equally out of the question for the tropics.

The everblooming groups can follow the weather and the soil and can maintain a foothold wherever these conditions are satisfactory or competition with other plants permit. In so far as records are available, it appears that everblooming plants are prevalent in the tropics, though, in accordance with Garner's theory, a species or variety might be everblooming there and be either everblooming or a spring or a fall flower in the temperate zone. Cold weather may delay growth and consequently delay flowering, and hot weather may hasten it, but if the light period is suitable for a particular plant it will flower as promptly as the climatic conditions permit, while if the light period is not suitable, weather changes cannot cause flowering. The apparently erratic behavior of certain plants brought to new areas of approximately similar climate is probably to be explained largely if not entirely as a length of day response, for even a difference of minutes may cause a change of growth.

VEGETATIVE RESPONSE TO LIGHT PERIODS

To recur to the recent experimental work on the responses of different plants to the length of the daylight period, the changes in the character of vegetative growth are as clear and as striking as is the change from the vegetative to the flowering behavior previously discussed. A common spring radish, the Globe variety, if exposed to a 7-hour day will continually enlarge its bulbous root at least for a year and probably indefinitely (plate 5, A). Similarly, the Irish potato, Jerusalem artichoke, and the yam develop tubers only under comparatively short days. Carrots, on the other hand, do not produce a bulbous root under a very short day but under a 14-hour day produce the typical carrot root, well stored with reserve food materials. The silverskin

onion produces a typical spring onion when grown under a 10-hour day, a slightly bulbous spring onion under a 13-hour day, and a typical summer onion bulb when grown under a 15-hour day (plate 5, B). In general, it appears that plants differ in the light period best suited to the production of reserve food supplies whether these reserves are developed as corns, bulbs, or tubers, or as resting buds. In no case in these experiments has the light period best adapted to formation of bulbs or other reserves of food material coincided with the daylight period best adapted for upward or top growth of the particular plant under consideration. In this particular the depositing of reserve food apparently differs from the flower response for it is not impossible for the daylight period suitable for flowering and for upward or top growth of a plant to coincide or at least to materially overlap. Comparison of Baldwin apple seedlings with seedlings of the box-elder emphasizes a wide difference of the optimum light exposure for upward growth. These apple seedlings grow most vigorously when exposed to approximately 10 hours of light daily and their growth is seriously depressed with extension of the light period to 14 or 15 hours (plate 6, A). It is not noticeably affected by a light period even much shorter than 10 hours. The box-elder, however, is scarcely able to grow at all with a day as short as 10 hours and makes its most vigorous growth when exposed to a 14- or 15-hour day (plate 6, B).

With these seedling trees, as well as with several other plants, it seems possible not only to depress vegetative growth but actually to carry this depression to the point of killing the plant merely by adjusting the light period to one extremely unfavorable for vegetative growth. As might be expected, there are numerous

species of plants for which no light period has yet been found that will completely suppress vegetative growth unless associated with fruiting and maturity. The classical idea of the normal death of a plant, especially as applied to annuals, is that death should occur following the maturation period which accompanies flowering and fruiting. While there is a very clear correlation existing between the fruiting of annuals and their immediately subsequent death, this is clearly not a necessary sequel. With many annuals, for example, the beggar tick, after flowering and fruiting has begun, a change of the light period to one more suitable for vegetative growth than for flowering will re-establish vigorous vegetative growth which within the limits of these experiments at least may be indefinitely prolonged. The death of annuals following their fruiting therefore would appear to be largely a reaction to an unfavorable length of day for vegetative growth exaggerated by the weakening of the plant through the strain of formation of flowers and development of seed. In both the box-elder and the Baldwin apple seedlings and in the case of the sumac, tulip-poplar, etc. leaf-fall can be brought about by shortening the day regardless of the favorableness of temperature and moisture conditions, while leaf-fall can be completely prevented throughout the winter if the short days of winter are supplemented by the use of electric light (plate 7, A and B). The distinction between evergreens and deciduous perennials may be therefore an expression of the reaction of these plants to the length of day prevailing in the latitudes in which they naturally occur.

PHYSIOLOGICAL SIGNIFICANCE OF LIGHT AND OTHER FACTORS

It is not the intention of the authors of these experiments to indicate that light is in itself the sole cause of the remarkably

diverse growth effects that result from changes in the light period. The length of day reaction is rather to be regarded as one of the most important factors in controlling the normal physiology of growing plants by modifying the function or the activities of the plant cells. Some of the experiments briefly referred to have demonstrated the comparatively slight but consistent changes in acidity of the cell sap in different portions of the plant as a result of the changes of length of day and these changes in acidity are directly correlated with the changes in the growth habits. In the case of short-day plants, for example, abrupt transfer from a long day to a short day causes a sudden and sharp decrease in acidity in the region of most active growth; this usually occurring about 3 to 5 days after the change in light period has been made. This drop in acidity, which is believed to indicate definite transition from the vegetative to the flowering condition, is only temporary and is followed by an equally rapid rise to almost the original level of acidity. The acidity relations resulting from exposure to the long days of summer also occur when the short daylight period of winter is prolonged by use of electric light of low intensity.

To what extent similar changes can be influenced in the normal physiology of growing plants through changes in temperature and food supply must be left for future experiments. Apparently, however, as indicated earlier in this discussion, these factors even though they may be able to operate in some degree are for many plants less important and the reactions to them are less sharply definite than is the case with the effect of the duration of the daily period of light.

PHOTOPERIODISM AND PLANT BREEDING

To attempt to point out the practical significance of a new factor hitherto un-

recognized in biology is as useless as would have been the attempt to predict the wireless telegraph and telephone at the time of the discovery of Hertzian waves. With the proper understanding of this new principle of plant growth, however, it would seem that not only should the work of plant breeders be greatly simplified and clarified but the introduction of crops into new areas might be somewhat less a matter of chance than it is at present. Seed production, especially of highly specialized varieties of plants, should be greatly facilitated. A variety of tobacco, the Maryland Mammoth, is now established agriculturally solely through the utilization of the length of day response. In southern Maryland this

type of tobacco grows to an unusually large size, frequently producing more than 100 leaves to a single plant. Because of these characteristics this variety is greatly desired for southern Maryland conditions (plate 8, A). However, in Maryland, it usually does not flower at all, or flowering occurs so late that seed will seldom mature. As this variety of tobacco was found to be a short-day plant, (plate 8, B) the problem of securing seed is satisfactorily met by growing the seed crop in Southern Florida during the winter, for under that daylight period the Mammoth variety does not continue its vigorous giant growth but flowers and fruits in practically the same manner as other ordinary varieties of tobacco.

LITERATURE LIST

- (1) ABBE, CLEVELAND. 1905. A first report on the relations between climates and crops. U. S. Dept. Agr. Weather Bur. Bul. 36.
- (2) ADAMS, J. 1923. The effect on certain plants of altering the daily period of light. *Annals Bot.* 37:75-94.
- (3) ALLARD, H. A. 1919. Gigantism in *Nicotiana tabacum* and its alternative inheritance. *Amer. Nat.* 53:218-233.
- (4) ANONYMOUS. 1924. Electric light and sunlight for plants. *Jour. Franklin Institute* 198:84.
- (5) ASTRUC, A. 1903. Recherches sur l'acidité végétale. *Ann. Sci. Nat. Bot., sér. 8*, 17:1-108.
- (6) ATKINS, W. R. G. 1922. The hydrogen ion concentration of plant cells. *Sci. Proc. Roy. Dublin Soc.*, n.s. 16:414-426.
- (7) BAILEY, L. H. 1891. Some preliminary studies of the influence of the electric arc light upon greenhouse plants. *N. Y. Cornell Agr. Exp. Sta. Bul.* 30.
- (8) ———. 1892. Second report upon electrohorticulture. *N. Y. Cornell Agr. Exp. Sta. Bul.* 42.
- (9) ———. 1893. Greenhouse notes for 1892-93. I. Third report upon electrohorticulture. *N. Y. Cornell Agr. Exp. Sta. Bul.* 55.
- (10) BERNARD, NOEL. 1902. Etudes sur la tubérisation. *Rev. Gen. Bot.* 14:5-25; 58-71; 101-119; 170-183; 219-234; 269-279.
- (11) BERNARD, NOEL. 1902. Conditions physiques de la tubérisation chez les végétaux. *Compt. Rend. Acad. Sci. (Paris)*, 135:706-708.
- (12) BONNIER, GASTON. 1895. Influence de la lumière électrique continue sur la forme et la structure des plantes. *Rev. Gen. Bot.* 7:241-257; 289-306; 332-342; 409-419.
- (13) BOUCHÉ. 1875. [Ueber das Clandestinitäten und Verkümmern der Blüten.] *Bot. Ztg.* 33:122.
- (14) BOVIS, W. T. 1915. A direct reading potentiometer for measuring and recording both the actual and the total reaction of solutions. *Jour. Med. Research* 33 (n.s. 28): 295-322.
- (15) BRIGGS, LYMAN J., and SHANTZ, H. L. 1916. Hourly transpiration rate on clear days as determined by cyclic environmental factors. *Jour. Agr. Res.* 5:583-649.
- (16) ———. 1917. Comparison of the hourly evaporation rate of atmometers and free water surfaces with the transpiration rate of *Medicago sativa*. *Jour. Agr. Res.* 9:277-292.
- (17) CHANDLER, W. H. 1914. Sap studies with horticultural plants. *Mo. Agr. Exp. Sta. Res. Bul.* 14.
- (18) CLEVELAND, CLINTON B. 1919. Hydrogen-ion concentration of plant juices. *Soil Sci.* 8: 217-242.
- (19) CORBETT, L. C. 1899. A study of the effect of incandescent gas light on plant growth. *W. Va. Agr. Exp. Sta. Bul.* 62.

- (20) COVILLE, FREDERICK V. 1920. The influence of cold in stimulating the growth of plants. Jour. Agr. Res. 20:151-160.
- (21) FLAMMARION, CAMILLE. 1898(?). Physical and meteorological researches, principally on solar rays, made at the Station of Agricultural Climatology at the Observatory of Juvisy. Exp. Sta. Rec. 10:103-114, 203-213.
- (22) GARNER, W. W., ALLARD, H. A., and FOUBERT, C. L. 1914. Oil content of seeds as affected by the nutrition of the plant. Jour. Agr. Res. 3:227-249.
- (23) GARNER, W. W., and ALLARD, H. A. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agr. Res. 18:553-606.
- (24) ———. 1921. Flowering and fruiting of plants as controlled by length of day. U. S. Dept. Agr. Yearbook 1920:377-400.
- (25) ———. 1923. Further studies in photoperiodism, the response of the plant to relative length of day and night. Jour. Agr. Res. 23:871-920.
- (26) GARNER, W. W., BACON, C. W., and FOUBERT, C. L. 1914. Research studies on the curing of leaf tobacco. U. S. Dept. Agr. Bul. 79.
- (27) GIROU DE BUZARINGUES, CH. 1831. Suite des expériences sur la generation des plantes. Ann. Sci. Nat. 24:138-147.
- (28) HAAS, A. R. C. 1920. Studies on the reaction of plant juices. Soil Sci. 9:341-368.
- (29) HAYNE, BENJAMIN. 1815. On the deoxidation of the leaves of *Cotyledon calycina*; in a letter to A. B. Lambert, Esq., Vice President of the Linnean Society. Trans. Linn. Soc., London 11:213-215.
- (30) HOFFMAN, H. 1882. Thermische Vegetation-constanten; Sonnen- und Schattentemperaturen. Ztschr. österr. Gesell. Met. 17:121-131.
- (31) ———. 1886. Phanologische Studien. Met. Ztschr. 3:113-120.
- (32) KARLING, JOHN S. 1925. A preliminary account of the influence of light and temperature on growth and reproduction in *Chara fragilis*. Bul. Torrey. Bot. Club 51:469-488.
- (33) KERBLE, FREDERICK. 1910. Plant-Animals. A Study in Symbiosis. Cambridge Press.
- (34) KINMAN, C. F., and MCLELLAND, T. B. 1916. Experiments on the supposed deterioration of varieties of vegetables in Porto Rico, with suggestions for seed preservation. Porto Rico Agr. Exp. Sta. Bul. 20.
- (35) KLEBS, GEORG. 1918. Über die Blütenbildung von *Sempervivum*. Flora, N. F. B. 11/12: 128-151.
- (36) KLEBS, GEORG. 1913. Fortpflanzung der Gewächse. 7. Physiologie. Handwörterbuch Naturwiss 4:276-296.
- (37) KRAUS, GREGOR. 1884. Ueber die Wassertheilung in der Pflanze. IV. Die Acidität des zellsaftes. Abhandl. Naturf. Gesell. Halle, 16:141-205.
- (38) LAURENT, ÉMILE. 1887. Recherches expérimentales sur la formation d'amidon dans les plantes aux dépens de solutions organiques. Bul. Soc. Roy. Bot. Belg. 26: 243-270.
- (39) LEWIS, I. F. 1914. The seasonal life cycle of some red algae at Woods Hole. Plant World 17:31-35.
- (40) LIEBIG, JUSTUS. 1842. Die organische Chemie in ihrer Anwendung auf Agricultur und Physiologie. Aufl. 4. Braunschweig.
- (41) LINSSER, CARL. 1867. Die periodischen Erscheinungen des Pflanzenlebens in ihrem Verhältniss zu den Wärmeerscheinungen. Mém. Acad. Imp. Sci. St. Petersb., s. 7, t. 11, no. 7.
- (42) ———. 1869. Untersuchungen über die periodischen Lebenserscheinungen der Pflanzen. Zweite Abhandlung. Mém. Acad. Imp. Sci. St. Petersb., s. 7, t. 13, no. 8.
- (43) LIVINGSTON, BURTON E. 1906. The Relation of Desert Plants to Soil Moisture and to Evaporation. Carnegie Inst. Wash. Pub. 50.
- (44) ——— and BROWN, WILLIAM H. 1912. The relation of the daily march of transpiration to variations in the water content of foliage leaves. Bot. Gaz. 53:309-330.
- (45) LODEWIJKS, J. A., JR. 1911. Erbliehkeitsversuche mit Tabak. Ztschr. Induk. Abstam. u. Vererb. 5:139-172; 285-323.
- (46) LOEB, JACQUES. 1922. The explanation of the colloidal behavior of proteins. Science, n.s. 56:731-741.
- (47) LUBIMENKO, V., and SZEGLOFF, O. 1923. Sur l'adaptation des plantes à la durée de la période claire de la journée. Compt. Rend. Acad. Sci. (Paris) 176:1915-1918.
- (48) MACDOUGAL, DANIEL TREMBLY. 1903. The influence of light and darkness upon growth and development. Mem. N. Y. Bot. Gard. 2.
- (49) ———. 1920. Hydration and Growth. Carnegie Inst. Wash. Pub. 297.
- (50) MAGROU, JOSEPH. 1921. Symbiose et tubérisation. Ann. Sci. Nat. Bot. sér 10, 3: 181-296.
- (51) MARCOVITCH, S. 1923. Plant lice and light exposure. Science, 58:537.

- (52) MAYER, ADOLF E. 1875. Ueber die Bedeutung der organischen Säuren in den Pflanzen. Landw. Vers. Stat. 18: 410-452.
- (53) ———. 1878. Ueber die Sauerstoffausscheidung einige Crassulaceen. Landw. Vers. Stat. 21: 277-347.
- (54) ———. 1884. Kleine Beiträge zur Frage der Sauerstoffausscheidung in den Crassulaceenblättern. Landw. Vers. Stat. 30: 217-226.
- (55) MCCLELLAND, T. B. 1924. The photoperiodism of *Tephrosia candida*. Jour. Agr. Res. 28: 445-460.
- (56) MCPHER, HUGH. 1924. The influence of environment on sex in hemp, *Cannabis sativa* L. Jour. Agr. Res. 28: 1067-1080.
- (57) MOBUS, M. 1892. Welche Umstände befördern und welche hemmen des Blühen der Pflanzen. Biol. Centbl. 12: 609-624, 673-687.
- (58) MOLLARD, MARIN. 1903. Sur l'obtention de bulbes chez l'oignon en cultures aseptiques. Bul. Soc. Bot. France 50: 631-633.
- (59) ———. 1907. Action morphogénique de quelques substances organiques sur les végétaux supérieurs. Rev. Gen. Bot. 19: 241-291; 329-349; 357-391.
- (60) MOORE, CHARLES A. 1908. The soy bean. A comparison with the cowpea. Tenn. Agr. Exp. Sta. Bul. 82.
- (61) NIGHTINGALE, G. T. 1922. Light in relation to the growth and chemical composition of some horticultural plants. Proc. Amer. Soc. Hort. Sci. 1922: 18-29.
- (62) OAKLEY, R. A., and WESTOVER, H. L. 1921. Effect of the length of day on seedlings of alfalfa varieties and the possibility of utilizing this as a practical means of identification. Jour. Agr. Res. 21: 599-608.
- (63) PURIEVICH, K. 1893. Die Bildung und Zersetzung der organischen Säuren bei den höheren Pflanzen. Kiew. Russian original not seen. Abs. in Bot. Centbl. 58: 368-374. 1894.
- (64) RANBY, F. WILLIAM. 1894. Electrohorticulture with the incandescent lamp. W. Va. Agr. Exp. Sta. Bul. 37.
- (65) REAUMUR, R. A. F. DE. 1738. Observations du thermomètre, faites à Paris pendant l'année MDCCXXXV. Comparées avec celles qui ont été faites sous la ligne, à l'Isle de France, à Alger, et en quelques unes de nos Isles de l'Amerique. Hist. Acad. Roy. Sci. (Paris). Mém. Math. & Phys., ann. 1735, p. 545-376.
- (66) REED, HOWARD S. 1919. Certain relationships between the flowers and fruits of the lemon. Jour. Agr. Res. 17: 153-165.
- (67) ———. 1921. Growth and sap concentration. Jour. Agr. Res. 21: 81-98.
- (68) RICHARDS, HERBERT M. 1915. Acidity and Gas Interchange in Cacti. Carnegie Inst. Wash. Pub. 209.
- (69) RIVERA, VINCENZO. 1920. Fattori biologici di rendimento agrario nel mezzogiorno. Riv. di Biol. 2: 153-172.
- (70) SCHAEFFNER, JOHN H. 1923. The influence of relative length of daylight on the reversal of sex in hemp. Ecology 4: 323-334.
- (71) SCHERTZ, F. M. 1921. A chemical and physiological study of mottling of leaves. Bot. Gaz. 71: 81-130.
- (72) SCHÜBBLER. 1879. The effects of uninterrupted sunlight on plants. (Abstract.) Nature 21: 311-312.
- (73) SPOHR, H. A. 1914. The Photolysis of Plant Acids. Carnegie Inst. Wash. Yearbook 12 (1913). 82-83.
- (74) TIMCKE, M. A. 1924. Effect of length of day on flowering and growth. Nature 114: 350-351.
- (75) TOURNOIS, J. 1911. Anomalies florales du houblon japonais et chanvre déterminées par des semis hâtifs. Compt. Rend. Acad. Sci. [Paris] 153: 1017-1020.
- (76) ———. 1912. Influence de la lumière sur la floraison du houblon japonais et du chanvre. Compt. Rend. Acad. Sci. [Paris], 155: 297-300.
- (77) VÖCHTING, HERMANN. 1887. Ueber die Bildung der Knollen. Cassel. Bibliotheca Bot. Heft. 4.
- (78) ———. 1902. Ueber die Keimung der Kartoffelknollen. Bot. Ztg. 60: 87-114.
- (79) VAISS, HUGO DE. 1884. Ueber die periodische Säurebildung der Fettepflanzen. Bot. Ztg. 42: 337-344; 353-358.
- (80) WANN, FRANK B. 1925. Some of the factors involved in the sexual reproduction of *Marchantia polymorpha*. Am. Jour. Bot. 12: 307-318.
- (81) WANNER, H. M. 1922. Photoperiodism of wheat; a determining factor in acclimatization. Science, 56: 313-315.
- (82) WARBURG, OTTO. 1886. Ueber die Bedeutung der organischen Säuren für den Lebensprozess der Pflanzen (Speziell der sog. Fettepflanzen). Unters. Bot. Inst. Tübingen 2: 52-150.
- (83) WISSENER, J. 1907. Der Lichtgenuss der Pflanzen. ... Leipzig.

A**B**

A. Violet. Plant at left in flower shows the characteristic behavior under the relatively short days of spring and fall. The plants in the center and at the right were exposed to electric light from sunset till midnight as a supplement to winter daylight. Beginning January 30, however, the daily light period of the center plant was reduced to $\frac{1}{2}$ hours. In a few days there was partial loss of rigidity in the leaf stems, resulting in the prostrate condition to be noted in the photograph. Subsequently the characteristic blue blossoms of spring appeared in this plant. This prostrate type of development is a characteristic feature in the development of many plants under short day conditions. Photographed April 17.

B. Biloxi soybeans. Plants at left exposed to a 12-hour light day. Plants at right exposed to 10 hours of light in two daily periods separated by 4 hours of darkness, thus giving the effect of a 14-hour light day. If the 10 hours of light had been continuous, these plants would have flowered and fruited before those at the left.



A. Cuscuta. Photographed November 1. Plants in exposure, at plants grown in light. B. S. S. O. O. O. Plants at light in exposure which began June 27. Plants in light which appeared on these plants October 1.

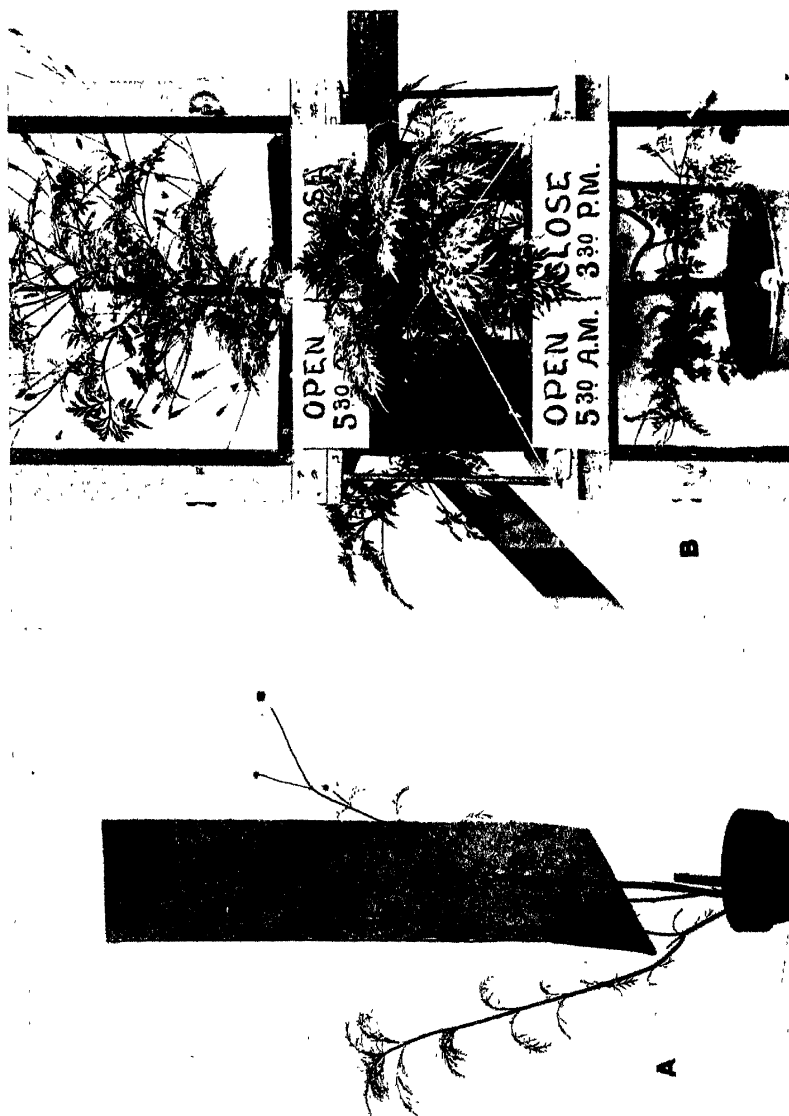
under short day length of winter about 9 1/2 hours) flowered December 22. Under long day exposure of 15 feet of light.

Under period, supplemented with electric light from sunset till midnight, throughout the period, when they were given 12 hour daily light exposure. For the blossoms



A Goldenrod Plant at left received electric illumination from sunset until midnight in addition to the winter days. Plant in center received natural day length, which by March had increased sufficiently to start the growth of flowering stems. Plant at right received only 7¹/₂ hours of light throughout the experiment.

B Lance cornopsis. Beginning Noember 1 seedling at left exposed to electric light from sunset to midnight in addition to natural day length. Flowering began May 1. Plant at right under natural length of day (about 14¹/₂ hours) shows no indications of flowering.



A. Common cosmos. The branch at right flowered promptly in response to the short winter day (about 9½ hours) to which it was exposed. The branch at left of screen remained sterile and continued to grow in response to the added electric illumination from sunset till midnight.

B. Yellow cosmos, the upper and lower portions of which were placed in light-proof chambers on July 11 and thereafter received 10 hours of light daily, while the central portion continued to receive the light of the entire summer day (about 14 hours). Both top and bottom of the plant responded in characteristic manner to the short day and soon flowered, as shown in the photograph. The central portion, on the other hand, remained vegetative in response to the long day.



A. Globe radish, given daily light of 7 hours. About 6 months old.

B. Silverskin onion plants from sets planted May 19, when the day is about 14½ hours long. Plant at extreme left is representative of a series exposed to the full seasonal length of day out of doors. These plants flowered in July, formed bulbs, and passed through the usual summer rest period after the tops had died down. In the series represented by the second plant from the left, which was exposed to a 13-hour day, the growth of tops was much greater while the bulb was delayed in forming and was reduced in size. The plant in center is representative of those exposed to a 10-hour day. In this case there is no summer rest period and no bulb is formed, the tops remaining green indefinitely. The individual at extreme right shows the behavior of plants grown under the natural length of day in the greenhouse, where the temperature was considerably higher than out of doors. The behavior was the same as that of the controls in the open except that the size attained was materially reduced. With the addition of electric illumination from sunset till midnight in the greenhouse only a slight attenuating effect was observed, as shown by the second plant from the right.

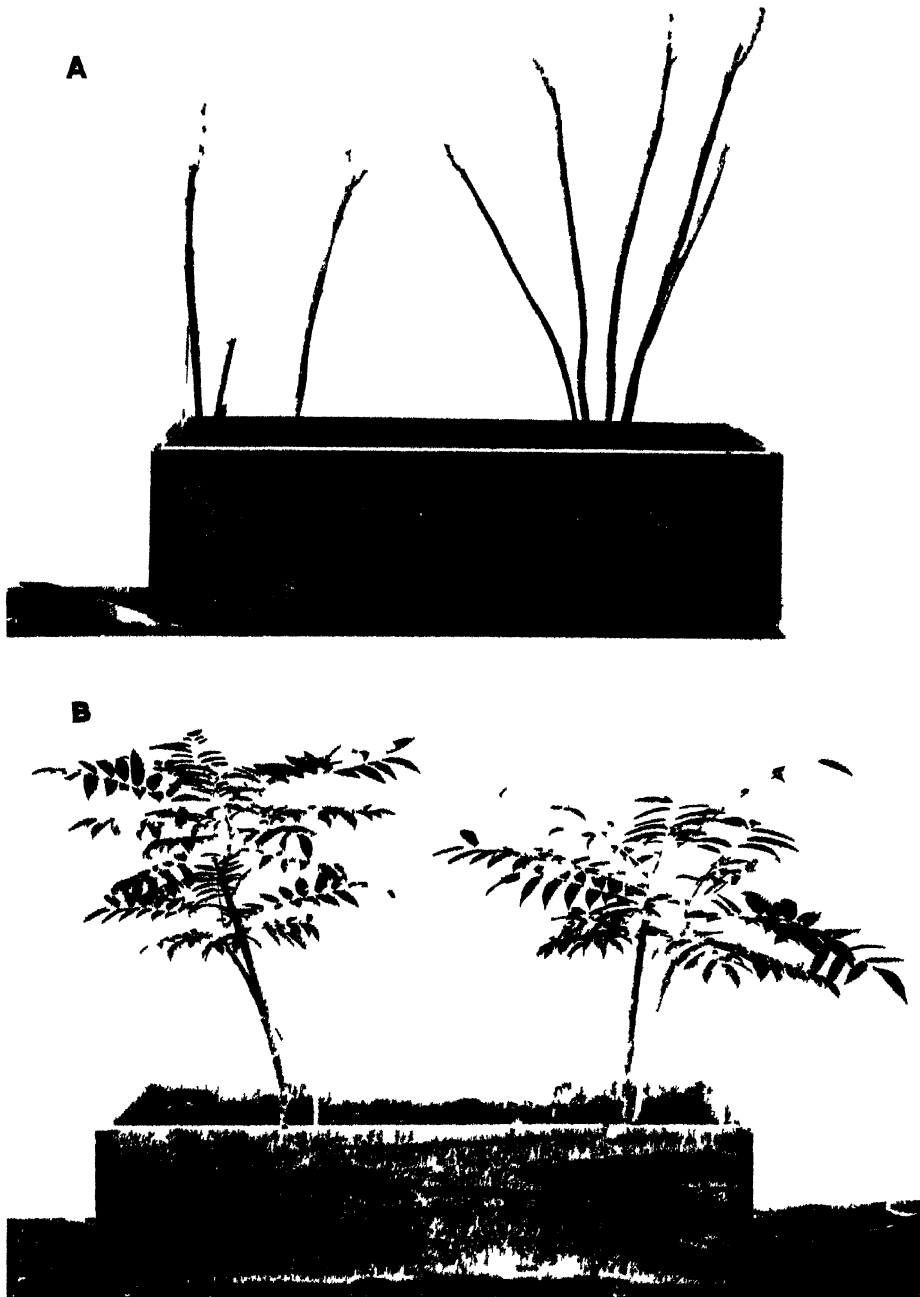


B



A Seedlings of Baldwin apple. Plants at right were exposed to 10 hours of light daily during the summer months, those on left received the full daylight exposure of summer. It is apparent that growth is more rapid and vigorous with only 10 hours of light daily than with the 14 to 15 hours of daylight of summer in the latitude of Washington. This would indicate a tendency toward an increased rate of growth with decrease in latitude.

B Seedlings of box elder. The plants at left were exposed to 10 hours daily while the plants at right were exposed to the full day length of summer. It is obvious that in contrast with the apple this species grows vigorously under long day conditions.



A Sumac. These plants were transplanted in April and remained out of doors till September 8, when they were transferred to the greenhouse. They received the full seasonal length of day throughout the test. The leaves were shed at about the usual time, and the plants remained dormant till spring.

B Sumac treated in all respects like the plants in A, except that when transferred to the greenhouse in September the trees received electric illumination from sunset till midnight. The leaves were retained through the winter.

A



B



A. Crop of Maryland Mammoth tobacco growing in southern Maryland where the plants seldom flower or mature seed.

B. Maryland Mammoth tobacco. The plant at the left received only the daylight period of the winter day in the greenhouse; the plant at the right was grown under the same conditions, except that the light period was lengthened by the use of electric light, and the condition of the summer day in Maryland thus stimulated.



RECENT DISCOVERIES IN THE BIOLOGY OF AMEBA

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THE ameba, from the moment of its discovery to the present, has stirred the imagination of biologists. Roesel von Rosenhof, that indefatigable amateur naturalist, who first saw and described a large ameba in 1755 (*der kleine Proteus*) was fascinated by this extraordinary creature which was so different from any living thing he had seen before, for, he says, he "frequently spent two or three hours in observing it." He saw and described the more conspicuous characteristics of the ectoplasm and the endoplasm, the crystals, the manner of movement and, surprisingly enough, he records and figures a case of reproduction by division, and relates how he performed microdissection on an ameba by means of a sharply pointed quill. This must be considered a most excellent contribution to the knowledge of the ameba by a man whose profession was the wholly unrelated one of miniature painting and whose hobby was not protozoa but insects.

The word "ameba" is used as a common noun in this and my previous papers to refer in a general way to any or all of the species of the several dozen genera comprised under the sub-order *Amoebæa*. A review of recent work on the ameba will perhaps be more illuminating if one recalls something of the historical background for the numerous investigations on this organism within the past few decades, for the ameba and its immediate relatives have figured prominently in the development of some of the most impor-

tant principles underlying the science of biology. Let us therefore continue for a few moments the historical account of how the ameba has come to be one of the classic organisms for the investigation of the fundamental properties of protoplasm.

After Roesel, nothing of importance was added to the knowledge of the ameba until it came under the eye of the great French naturalist Dujardin in 1841, who, because of his studies of the pseudopods of amebas and foraminifera, made the profound discovery that the gelatinous substance of these organs, the protoplasm, is the physical basis of life. For boldness of conception, far reaching significance and liberating quality, this remarkable concept may well be considered without a parallel in the history of biology. It required the living matter in its pure form, so to speak, as it is observed in amebas and foraminifera to disclose the great fundamental truth that was destined to destroy the mass of mystical and fanciful notions which for a long time had kept the study of living organisms from becoming scientific.

This discovery inevitably began to transform biology from a study of organisms as a collection merely, of curious or interesting objects, to the serious study of the properties of living matter. With the extension of Dujardin's conception by Max Schultze, another great student of the rhizopods, who demonstrated the general identity of plant and animal protoplasm, the ameba, as indeed every other organism, could be studied not merely to

understand that organism, but to explain at the same time the manifestations of protoplasm in any plant or animal whatsoever.

It required, however, the establishment of the principle of evolution to justify completely the method of reasoning from one organism to another with respect to the properties of living matter. The present-day biologist would no more think of questioning the soundness of this form of reasoning than he would question the validity of the multiplication table. Every organism is a "flower in the cranied wall."

With the general acceptance of the principle of evolution the amoeba suddenly became the centre of new interest, for, because of its extremely simple structure, it necessarily found itself at the root of the family tree representing the primitive ancestor of man and the animals; and it naturally became of great importance theoretically, therefore, to know more about the structure and especially the physiology and the behavior of this living representative of the most ancient ancestor of man.

The most distinctive property of the amoeba is of course its peculiar manner of movement due to protoplasmic streaming, but this property which was first described by Roesel, was later found to be present in greater or less degree in the protoplasm of a great many other organisms, plants as well as animals; and it is now supposed by many zoologists to be essential in the embryological differentiation of the higher animals. The results of investigations on amoeboid movement therefore have always been of very wide interest, and this phenomenon is still best studied in the amoeba. Many physiologists also hold that the simplest form of muscular contraction, as well as ciliary and flagellar contraction, is some form of amoeboid

movement and every contribution to the knowledge of amoeboid movement is believed also to contribute to an explanation of these forms of contraction. And finally, the discovery of a number of parasitic species of amoebas has greatly increased the interest in these organisms from still another point of view. Because of the prominent part the amoeba has thus played in the development of the basic conceptions of zoology, it takes its place with the dog and the frog in the great "Zoological Trinity," as outstanding inspirers of basic research.

CYTOPLASMIC DIFFERENTIATION.

In a discussion of the recent advances in the knowledge of the structure of the amoeba, it may be well to take up first those parts of its morphology which were discovered first, namely, the ectoplasm and the endoplasm. Here, unfortunately, confusion has arisen as to the meaning of these two words. Thus the word ectoplasm is used to denote, for example; 1, the outer clear layer of an amoeba as distinguished from the granular contents; 2, the outer stiffer layer; 3, the clear part of the outer stiffer layer; 4, clear protoplasm wherever it occurs in the amoeba. And by implication the endoplasm is, of course, in each case the rest of the protoplasm. Now it goes without saying that it is clearly in the interest of science to use these words with definite meanings, and in this case it seems best to follow the rule in such matters, namely, adopt the original meaning proposed for the words, if practicable. Haeckel originally proposed the words and defined ectoplasm as the stiffer outer layer while endoplasm referred to the internal more fluid layer. These are the meanings adopted in this paper. In addition, the qualifying terms, "clear ectoplasm," "granular ectoplasm," etc., will be found useful, since there is

wide variation in the amount and distribution of granules in both the ectoplasm and the endoplasm of the various species of amebas.

The conversion of endoplasm into ectoplasm at the anterior end of an ameba and the reverse process at the posterior end, producing thus a kind of circulation as the ameba moves along, was first clearly enunciated by Bütschli, but the occurrence of this process in those amebas with a very stiff ectoplasm was questioned by Jennings ('04), who believed the ectoplasm to be something like a permanent sac in which the ameba rolled along, as it were. The evidence for this conclusion consisted largely in the observation of the movement of small particles on the surface of the ameba during locomotion. This quality of the ectoplasm has been investigated recently by Howland ('24), who used a microdissector in her work. Numerous experiments confirmed the generally accepted belief that the ectoplasm in *Thecamoeba (Amoeba) verrucosa* is very firm, a convincing demonstration consisting in rupturing the ectoplasm and then pulling it off the endoplasm in toto as one might pull an inverted sack off its contents. Howland also showed that ectoplasmic wounds heal rapidly and that large areas of new ectoplasm are made during every act of defecation. It had been observed before that ectoplasm is made and a little later destroyed, whenever a food cup is made for the purpose of eating a particle of food.

The change from ectoplasm to endoplasm and the reverse has also been subjected to experimental analysis, and aside from the effect of change of temperature which has often been noted to change the rate of ameboid movement, presumably by changing the viscosity of the protoplasm, it has been found that by mechanically agitating an ameba the ectoplasm in large

part can be transformed into endoplasm even though no locomotion takes place; and by injecting a trace of acid (HCl) into an ameba some endoplasm is transformed into ectoplasm, while the injection of a trace of alkali (NaOH) has the reverse effect (Chambers, '21).

It is of great interest of course to know what factors are concerned in the conversion of ectoplasm into endoplasm and the reverse, since neither the morphology of the ameba nor its characteristic form of movement can be understood unless these factors are known. And it is also recognized that an understanding of the relation between ectoplasm and endoplasm will go far in furnishing an explanation of similar changes in the protoplasm of many other animals and plants, especially in animal eggs at the time of fertilization, mitosis, cleavage, etc. The general problem has therefore been attacked in a number of organisms by experimental methods. The earlier tentative hypothesis in explanation of the difference between ectoplasm and endoplasm was based on a difference in viscosity, which was generally assumed to be brought about normally by some metabolic process, in analogy to changes in viscosity occurring in inert fluids such as pitch, solutions of gelatin and the like. The explanation seemed satisfactory enough while this subject was still in the observational stage; but when the matter began to be tested experimentally by means of micro-manipulators in the hands of Kite and Chambers and in various other ways by Hyman, Spek, Heilbrunn and a number of other investigators, it was found that the results of this work did not seem consistent, probably because they did not fall in line with the prevalent simple assumption based on a difference of viscosity. To illustrate: it has been observed that amebas move more slowly

as the temperature is decreased from the optimum towards zero. Many viscous fluids, molasses for example, do the same at the same temperature. One may assume, therefore, as has been done, that the slowing down in the rate of movement is caused merely by a difference in viscosity as a direct result of changes in temperature. But it requires energy to move protoplasm, and this is of course derived from some form of metabolism, that is, chemical change. Now it is also known that such chemical changes as are likely to occur in protoplasm, occur less rapidly or less extensively in lower than in higher temperatures. It is possible therefore that at least a part of the effect of the slowing down of movement with a decrease of temperature is due to a decreasing amount of available energy, and that the temperature effect on viscosity is, to a considerable extent, an indirect effect. There is a considerable body of data bearing on this general subject consisting mostly of isolated observations, but so far it has not been possible to interpret them satisfactorily from a single point of view.

PLASMA MEMBRANE

In addition to the ectoplasm and the endoplasm, which can be distinguished from each other by their physical consistency, there is an extremely thin outer fluid layer on the ameba which can be demonstrated satisfactorily only by its power of carrying small particles adhering to it, toward the anterior end of a moving pseudopod (Schaeffer, '20). Observations and measurements on the activities of this layer indicate that it is the plasma membrane or at least a part of it, and therefore of great physiological interest. It is one of the very few cases where a visible demonstration of this membrane is possible. Since this layer has mistakenly been supposed, in some instances, to include some or all of the stiffer ectoplasm lying

immediately underneath, it may be well to state the essential characteristics of this layer as determined by observation (fig. 4).

First, it has been found to exist in a large number of species of amebas of various sizes and shapes. Second, its existence as a structure distinct from the ectoplasm is shown by the fact that particles adhering to it on the outside are seen to move forward over the stationary crystals or other granules imbedded in the ectoplasm, and especially by the rate of movement which in some species (*Thecamoeba sphaeronucleosus*) may be as high as 3.5 times as fast as the ameba itself moves. Third, this layer over the entire free surface of the ameba moves toward the active anterior end at varying rates over different parts of the surface, while the ameba is in locomotion. The substance of the layer must therefore be continually destroyed at the active anterior end of the ameba and be continually recreated at the posterior region of the ameba. Fourth, the layer is extremely thin, being probably less than one micron in thickness. Accurate measurements are difficult to make directly owing to its extreme thinness and to diffraction of the light at the sides of the ameba. The substance of the layer is presumably protoplasmic, and the cause of the movement, if it is a surface tension effect, is due rather to an increase of tension at the anterior end than a decrease in the posterior region, since in those amebas which form ectoplasm to a greater or less extent over the anterior half of the body, the particles move toward the anterior end much less rapidly than in those amebas which form ectoplasm only at the anterior edge.

VARIATIONS IN PSEUDPODS

One of the most interesting features of the structure of amebas is found in the varied size and shape of the pseudopods,

although we have at present little more than descriptive knowledge of these organs. For convenience of discussion it is well to characterize certain more or less distinctive features of pseudopods by descriptive names. In the first place it is desirable to restrict the name pseudopod to extensions of protoplasm on an ameba greater than a hemisphere. Lesser extensions constantly occur in all amebas and it would be an aid to clearness of description to call these extensions "waves," as some writers, in fact, do. Again, for the sake of clearness, it is not advisable to use the name pseudopod in referring to the whole of a limax ameba; even in amebas it is desirable to indicate whether one is speaking about the whole of one or only a part of the animal.

For a full discussion of the name of the common large ameba (*Chaos diffilans* Müller—*Amoeba proteus* Pallas emend. Leidy emend. Schaeffer) reference may be made to my paper, 1926 Carnegie Institution of Washington Publications, No. 345; and for description of the species reference may be made to my earlier paper ('17) and book ('20). The 1926 paper also contains observations on a number of other species and genera mentioned in the present paper. One cannot observe this ameba in normal movement without noticing that at practically all times some one pseudopod is the main pseudopod through which the ameba flows on. A series of camera lucida sketches of the ameba at intervals of half a minute, for half an hour, illustrates very graphically the presence of a main pseudopod which may preserve its identity for half an hour or more while all other pseudopods within a minute or two after formation are withdrawn. This form of ameboid movement, far from being the general method of locomotion among amebas, is in reality

found only in a very few species. A main pseudopod is in fact characteristic of only four other common species: *Metachaos discoides*, *M. annulata*, *M. gratum*, *M. laureata*.

If one sketches, by way of comparison, the form changes of another common large species (*Polychaos dubia*) in a similar way, it is seen that the pseudopods, which at first sight strongly resemble those of the amebas just mentioned, are really formed in quite a different way. No main pseudopod is distinguishable. This ameba, which usually resembles a hand with the fingers spread out, flows forward through two or more pseudopods at the same time, and keeps itself from dividing into several parts by forming web-like extensions continually between the bases of the pseudopods. Although at times one or other of the pseudopods flows more rapidly than the others and thus acquires the character of a main pseudopod, this distinction is only temporary. The torch of leadership is, as it were, continually passing from one to the other among the several leading pseudopods.

Both these types of pseudopods agree, however, in one important characteristic, namely, they increase in size sufficiently to permit the whole ameba to flow through them. That is, they are of *indeterminate* size.

In contrast to these amebas there are a large number of species which form pseudopods that never enlarge beyond a certain size, when they are withdrawn. Such *determinate* pseudopods are characteristic of a common fresh-water ameba of rather small size, *Mayorella bigemma*, and several species of marine amebas belonging to the same genus (fig. 1, d). The species *bigemma* is characterized by a triangular or polygonal body while in locomotion, with numerous conical pseudopods scattered over the anterior part of

the body. They are especially conspicuous along the anterior edge. The entire anterior edge of these amebas advances during locomotion although occasionally lobes develop through more rapid flowing of some part of the edge, producing in extreme cases a Y-shaped body. The polygonal shape is, however, quickly re-

microns and then are withdrawn or they may be continuously projected as small conical points, while the spaces between them advances in the form of a web, for considerable distances. These "false feet" might therefore better be looked upon as "toes" which lead the way in locomotion. There is some property in the

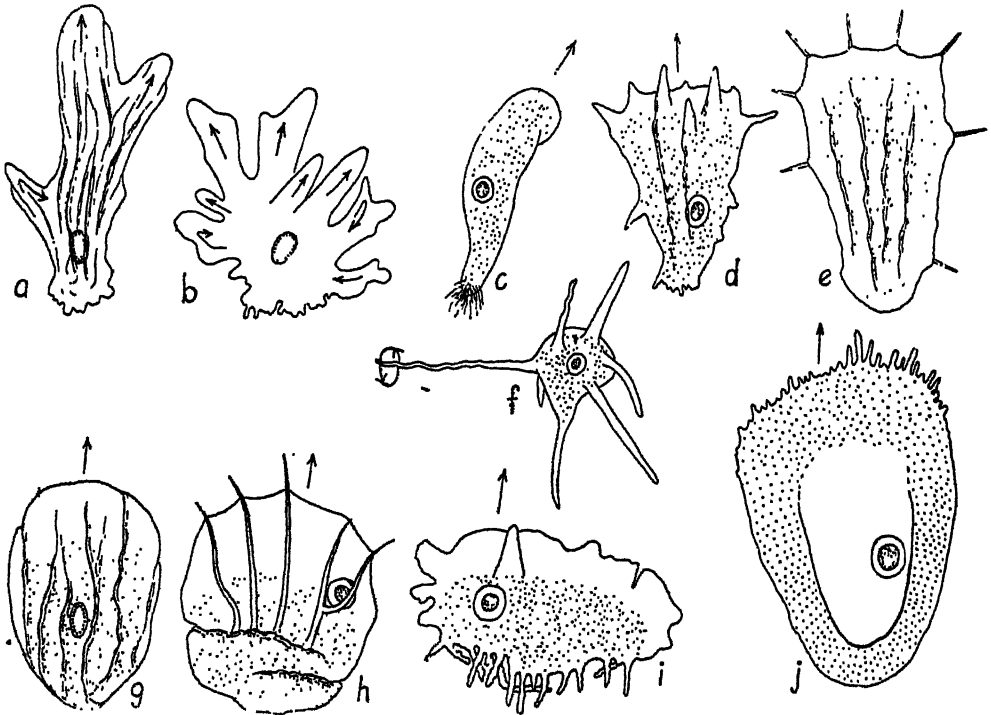


FIG. 1. SKETCHES OF DIFFERENT SPECIES OF AMEBAS TO SHOW VARIOUS KINDS OF PSEUDOPODS AND ECTOPLASMIC RIDGES

a, *Cbaos diffuens* (*Amoeba proteus*); *b*, *Polychaos dubia*; *c*, *Trichamoeba clava*; *d*, *Mayorella bigemna*; *e*, *Pontifex maximus*; *f*, *Astramoeba flagellipodia*; *g*, *Thecamoeba verrucosa*; *h*, *Hyalodiscus caeruleus*; *i*, *Flabellula citata*; *j*, *Coelilopodium gulosum*. Determinate pseudopods in *d*, *e*, *b*, *j*; indeterminate pseudopods in *a*, *b*. Note hair-like uroidal projections in *c*, and spiral pseudopod in *f*.

sumed again by the withdrawal of one of the limbs of the Y. The ameba thus changed its direction of movement by the unusual method of forming an indeterminate pseudopod. But while this was going on and at all other times of active movement, the advancing edge carried a dozen or more small conical pseudopods which enlarge to a length of 12 or 15

microns and then are withdrawn or they may be continuously projected as small conical points, while the spaces between them advances in the form of a web, for considerable distances. These "false feet" might therefore better be looked upon as "toes" which lead the way in locomotion. There is some property in the

protoplasm of this ameba which prevents the advancing wave of protoplasm between the conical pseudopods from catching up with the tips of the pseudopods. But the most perfect example of determinate pseudopods is found in a large marine ameba which is remarkable from several other points of view. In this ameba (*Pontifex maximus*) in which no

coördinated locomotion has been discovered, small needle-like pseudopods bristle out all over the animal, especially when disturbed (fig. 1, e). They resemble somewhat the spines of some cacti. The pseudopods are of clear protoplasm, about 12 microns long by 1 micron thick, and arise from a bulbous base. There is very little variation in size or shape. The first stage in the formation of these pseudopods is the extension of a thin tongue of clear protoplasm, projected into the water from a papilla of clear protoplasm. This tongue is of slightly irregular shape and may wave about slightly in the water. Very soon, however, it reaches the size indicated beyond which it cannot grow and then its protoplasm becomes set and the pseudopod becomes rigid. The protoplasm as it were, has filled the mold; there is nothing to do now but to withdraw. This process is accomplished by a softening of the protoplasm, whereupon the pseudopod becomes crooked and gnarled as it shrinks and finally disappears into the ameba. These determinate pseudopods, each of which represents about 1/100,000 or less of the bulk of the entire ameba, stand in strong contrast to the determinate pseudopods mentioned above which take in the whole ameba, and indicate important structural differences between the protoplasms of the two species of amebas.

The distinction between determinate and indeterminate pseudopods reaches over also into another activity of the ameba, that of eating. It is well known how the common large amebas eat by flowing around the food object, enclosing it in a food cup. One or more pseudopods may take part in the formation of a food cup depending upon the size and location of the food body (Kepner and Taliaferro, '17). But only indeterminate pseudopods can be used in the feeding process. Pseu-

dopods of limited size cannot adapt themselves to the formation of food cups, and amebas which form pseudopods of this character envelop their food by projecting broad waves of protoplasm over and around the food particle, as do also those amebas which form no pseudopods whatsoever (*Thecamoeba verrucosa*) (fig. 1, g). Since determinate pseudopods have been found not to take part in either of the two important activities of the ameba, locomotion and feeding, it is difficult to see what function, if any, they perform.

There is another type of small pseudopod which, although it is of determinate character, nevertheless possesses several distinctive qualities which sets it apart from the determinate pseudopods just mentioned. These small pseudopods are the small root-like projections of clear protoplasm which extend backwards from the posterior end of the amebas belonging to the genus *Trichamoeba* (fig. 1, c). These projections which may be referred to collectively as the uroid, apparently play a part in locomotion. It has been observed that these projections which are extremely difficult to see in many cases, are fastened to the substratum while the ameba is in locomotion and serve to keep the ameba, which is in clavate shape, from rolling over. But how these uroidal projections release their hold on the substratum and fasten down again, as they obviously must do during locomotion, has not been observed. It has been determined, however, that they may be formed very quickly and that they are probably present in all large clavate amebas with very "fluid" protoplasm. They vary in number from several score or more extremely thin hairlike projections to half a dozen or so larger rootlike and gnarled and, it may be, branched extensions, depending upon the species. These uroidal extensions are of course not to be confused

with the wrinkled remnants of withdrawing pseudopods frequently observed at the posterior region of many large amebas. The character of the uroid is a valuable characteristic in the determination of species.

It is usually assumed that pseudopods move only when or because endoplasm is flowing in or out of them, and this is undoubtedly typical of them. There are exceptions, however. An interesting case is the tentacle-like motility of the pseudopods found in the amebas belonging to the genus *Vexillifera*. These amebas project numerous pseudopods of the determinate type, resembling those of *Mayorella*, but there are usually some at the anterior edge much longer than the rest which wave about in the water more or less actively for 20 seconds or longer before they are retracted. Waving pseudopods are more frequently formed when locomotion has slowed down than when the ameba is moving actively.

Another interesting case of moving pseudopods is found in *Astramoeba flagellipodia*, in which the pseudopods are thrown into loose spirals of three or four turns and kept in motion (fig. 1, f). The tip of the pseudopod makes one revolution in about three seconds, the movement being like that of a flagellum. The body of the ameba of course remains stationary during these movements, which makes it clear that the spiral pseudopod is not like a rigid corkscrew being rotated on its long axis, but dynamic, the turns continually forming at the free end and disappearing at the base of the pseudopod. If such a process occurred rapidly the pseudopod would act like a propeller, pulling the ameba through the water. Theoretically, this kind of a pseudopod might perhaps be considered as a stage between the indeterminate pseudopod and a functional flagellum. Static spiral pseudopods are

occasionally observed in a number of species of amebas.

All the different kinds of pseudopods mentioned thus far can be projected freely into the water out of contact with a solid body. It remains now to mention the small pseudopods seen on many species of amebas around the periphery of the advancing sheetlike waves of protoplasm, which apparently are not projected freely into the water (fig. 1 j). These pseudopods are very difficult to see owing to their great transparency and minute size, being sometimes less than a micron in length. In other particulars, however, they resemble the conical determinate pseudopods described above. These pseudopods are observed most frequently among those amebas that move by means of thin waves of protoplasm, such as *Cochliopodium*, *Gibbodiscus*, *Hyalodiscus*, and some species of *Thecamoeba*.

"HAIRY" AMEBAS

Hairy frogs find their counterpart among the amebas, for there are three species of "hairy" amebas (Wailes; Schaeffer, '25). Two of these species have minute perpendicular hair-like extensions on the outer surface which in one of these species are about one micron long, extremely thin and arranged in a hexagonal pattern with the "hairs" placed one-half micron from each other. Of their nature nothing is known except that they persist after the death of the animal. Another species of ameba belonging to the genus *Pontifex*, has much longer projections. These are ten microns long and one micron thick and cover the outer surface so thickly as to resemble a coat of fur. This resemblance is heightened by the slightly matted appearance of the projections. The color of these projections is a light grayish brown which aids in completely obscuring the underlying protoplasm of the ameba

over considerable areas. These projections also persist after the death of the ameba.

ECTOPLASMIC RIDGES

The ridges which occur normally in the ectoplasm of a number of amebas form an important part in any general discussion of the ectoplasm, but comparatively little attention has been paid to these structures in the past few years. Leidy first gave a good description of the folds in the common large ameba and he also first saw the longitudinal walls of ectoplasm within the general endoplasmic stream. From that time to this, these important structures seem not to have been seen by a single author of a new theory of ameboid movement based upon this ameba, for no mention is made of them!

Longitudinal ectoplasmic ridges are found in a large number of species of amebas. In the family Thecamoebidae, to which the common *Thecamoeba verrucosa* belongs, longitudinal ridges are a family character, and a considerable number of species of the Mayorellidae possess ridges (fig. 1, d, g). Ectoplasmic ridges are not formed in the same way in all cases. In the Thecamoebidae the longitudinal parallel ridges are continually being prolonged at the anterior edge of the ameba and continually destroyed at the posterior end, while the ridges as such retain their identity for many minutes, as long in fact as the ameba retains a more or less straight path. In the Mayorellidae the ridges frequently develop as a buttress extending backwards from a conical pseudopod, which as has been stated above, frequently persists for a comparatively long time. The ridges in the common large ameba are formed in a different way again. In this species the ridges are formed mostly along the whole length at once, by a wave-like outpushing perpendicular to the long

axis of the ameba. Occasionally such ridges are prolonged at the anterior end for a short time, but only in rare cases is a ridge found to be as long as the ameba. The part of the ectoplasmic wall bordering on the ridge or lying between two ridges and not rising up with it becomes eventually one of the ectoplasmic walls within the endoplasm described by Leidy.

The width of these ridges is of considerable interest in a study of the general morphology of amebas. How small an ameba may be expected to show sufficient morphological differentiation to enable one to recognize it in the living state? Smaller, apparently, than any ameba now known. The ridges in a new species of marine *Thecamoeba* whose description has not yet been published, are only from 0.5 to 1 micron wide while the ameba itself is only 10 microns wide and long. Another new species closely related to it is 12 microns wide and possesses 3 to 5 characteristic ridges of about the same width. There seems to be no reason therefore why a ridge of the *Thecamoeba* type should not be found on an ameba as small as 2 or 3 microns, which is the lower size limit for known amebas. In other words there would seem to be no limit imposed upon the existence of recognizable morphological structures in the Thecamoebidae at least, upon which specific distinctions may be based.

This great array of organs which the ectoplasm can construct: the various kinds of pseudopods, uroids, ridges, ectoplasmic walls and "hairs," together with other structures and modifications not here mentioned, in the various species of amebas cannot fail to excite interest in this layer of extraordinary potentialities. The student of the physical properties of protoplasm in so far as form is concerned, can certainly find a rich supply of material in these structures for experimen-

tal work. The ectoplasm possesses its characteristic qualities, however, only because of its position; that is, the endoplasm which may at any moment become ectoplasm possesses the same qualities as the ectoplasm but in a latent form, as it were. But there are distinctive structures of various kinds found in the endoplasm which indicate the existence of still other properties in ameban protoplasm not exhibited by the ectoplasm. We may consider a few of these.

ENDOPLASMIC CRYSTALS

A very common inclusion of the endoplasm are the crystals. They occur in various sizes and shapes depending upon the species. They are found singly almost always, but in *Mayorella bigemma* they are always twinned. So far as known the crystals are enclosed in small watery vacuoles, each in its own vacuole. Their composition is not definitely known although it is believed that one of the phosphates of calcium is the chief, possibly the only constituent.

Curiously enough, the crystals were seen and described (Roesel, 1755) and measured (Ehrenberg, 1838) before the nucleus and the contractile vacuole were seen. After Ehrenberg, however, practically no notice was taken of the crystals until Penard ('02) in his great work on the rhizopods described crystals in several new species of amebas. But Penard was somewhat inclined to doubt whether crystals possessed characteristics stable enough to base specific descriptions thereon. It was found, however, by using the isolation pedigree method with three common species of amebas, that the characters of the crystals are characteristic of the amebas in which they occur, under ordinary conditions (Schaeffer, '17). In later studies a number of other species of amebas were found also to contain crys-

tals whose characteristics possess specific value. In this work a polariscope is very useful because the degree of optical activity of the crystals in at least some species of amebas varies somewhat if abnormal amounts of food are ingested, the crystals under these conditions becoming less clear and sometimes irregular. Most amebas carrying large crystals possess only one kind or size of crystal under average conditions; a few possess a second or a third kind in small number; while one species, the common *Polychaos dubia*, normally possesses at least four varieties, each of which varies within rather wide limits, the wide degree of variation furnishing here the specific crystal characteristic. In this species the bipyramidal variety predominates, sometimes almost to the exclusion of the other varieties, when food is very scarce and mostly of vegetable nature. In general, however, the crystals vary less under normal or adverse conditions than the pseudopods, the contractile vacuole or even the general shape of the nucleus. Under uniform general conditions the crystals remain uniform.

Very little is known about the origin, significance or fate of the crystals. There are general reasons for believing that they arise as by-products of metabolism and that they are to be regarded as waste products. No instances of the excretion of crystals are recorded, but on the contrary the number of crystals markedly increases in the larger species when division does not take place regularly, so that after a week or two the ameba is little more than a sac of crystals (Schaeffer, '20). This condition is usually fatal. It is probable therefore that crystals are never excreted and that their number is kept down by division of the ameba, reproduction thus being in effect, a form of excretion.

CONTRACTILE VACUOLES

One of the most conspicuous inclusions in the endoplasm of some of the larger fresh water amebas is the contractile vacuole, seen first by Ehrenberg in *Thecamoeba verrucosa*, although nothing of its true nature was recognized at the time. Subsequent observations gradually led to the generalization that fresh water amebas possess contractile vacuoles while salt water forms do not, but recent study of marine amebas has shown that several species of *Thecamoeba* possessing thick ectoplasm contain contractile vacuoles pulsating just like those in the fresh water species. And it was also found that a number of other marine species of amebas when transferred to fresh water formed contractile vacuoles within themselves which pulsated characteristically.

Of the actual structure of the contractile vacuole comparatively little is known. It has been established that the vacuole consists of a drop of fluid which slowly gathers in the endoplasm and is then at intervals emitted to the exterior through a small pore in the ectoplasm. The rate of contraction is much more irregular than that observed in the ciliates, but no detailed study seems to have been made of this function. It has been shown recently that the vacuole is enclosed in an extemporized membrane which preserves its identity when dissected out and placed in the culture medium (Howland).

METAPLASTIC GRAINS

The so-called "excretion spheres," "nutrition spheres" (Hayes), or "metaplastic grains" are another kind of inclusion within the endoplasm of a large number of species of amebas. These bodies, which range from a fraction of a micron to about 10 microns in diameter,

are usually of a bluish or greenish color of varying intensity, depending upon the species, and occur in varying number depending upon the amount of food available. Recently a study has been made by means of stains to learn more about the composition of these bodies, with the result that they seem to be composed mostly of starch (Hayes). It may be mentioned here that in the common large living ameba, these bodies move around slightly in the protoplasm, apparently of their own accord, resembling an exaggerated but slowed down Brownian movement (pedesis), a movement possibly due to differences in surface tension arising out of the deposition or solution of its substance. Similar spheres or grains are found in the pelomyxas, sometimes in large number (*Pelomyxa palustris*, *P. schiedti*), and especially in the parasitic amebas where very large bodies have been described under the name of glycogen. Whatever may be the exact nature of these bodies, there is general concensus of observation that they are reserve food bodies, that they increase in number during periods of abundance of food and decrease in number and size when food is scarce.

Whether the small grains in the peripheral zone of protoplasm of a number of species of *Cochliopodium* have a composition similar to the metaplastic grains mentioned above is doubtful, because the size of these grains seems to vary very little. These grains are roughly spherical, only a fraction of a micron in diameter and are difficult to see. They are of great interest because they are arranged in one layer only in the thin peripheral zone of otherwise clear protoplasm, at nearly equal distances from each other, in such a way as to lie in rows which radiate in curved lines with their origin in the central mass of protoplasm. The arrangement suggests that of the seeds in the outer

zone of a sunflower head. The peripheral zone of protoplasm is in constant movement while these amebas are in locomotion, nevertheless these grains maintain their arrangement as described. This phenomenon indicates the presence of physical forces in the granules or in the protoplasm which would hardly be suspected if the granules were not limited to one layer by the thinness of the protoplasm of the peripheral zone.

Numerous other kinds of inclusions occurring more or less frequently in the

is visible in the living ameba where the nucleus is single or double and not entirely obscured by food bodies. In color it is bluish green or greenish blue, of a somewhat more intense hue than the clear protoplasm, if the chromatin is evenly distributed. If the chromatin is unevenly distributed or exists in discrete grains, the color indicated attaches only to the chromatin. The nuclear membrane is always clear. The nucleus exists in three typical shapes: ovoidal, spherical and discoidal. The best examples of the

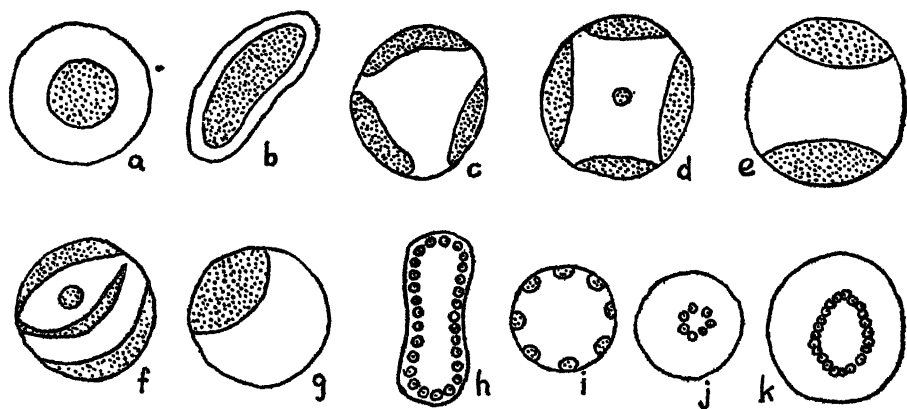


FIG. 2. SKETCHES ILLUSTRATING THE DISTRIBUTION OF PERIPHERAL CHROMATIN IN VARIOUS SPECIES OF AMEBAS, ALL EXCEPT *j* IN OPTICAL SECTION

In single central masses: *a*, *Flabellula citata*; *b*, *Thecamoeba hilla*; in irregular shaped islands on nuclear membrane: *c*, *Rugipes bilzi*; *d*, *Cochliopodium clarum*; *e*, *Thecamoeba munda*; *f*, *Karyamoebina falcata*; *g*, *Endamoeba nana*; in small grains: *h*, *Chaos diffluum*; *i*, *Chaos chaos*; *j*, *Councilmania muris*; *k*, *Mayorella bigemma*.

endoplasm such as permanent vacuoles, chromidia, chromatoidal bodies, zoochlorella, symbiotic bacteria, mitochondria, etc., cannot be discussed here with profit owing either to their infrequent occurrence or lack of definite knowledge about them.

NUCLEUS

The nucleus is of course the most important of the endoplasmic inclusions because of the essential part it plays in metabolism and reproduction. A nucleus

ovoidal shape are *Polychaos dubia*, whose nucleus is a stout regular ovoid; *Thecamoeba hilla*, whose nucleus has the shape of a slender ovoid that is almost kidney shaped; and *Trichamoeba caerulea* which has about 15 small regular ovoidal nuclei. Discoidal nuclei are found in *Metachaos discoides* and in the common large ameba. In the older and larger individuals of the latter species, the discoid nucleus sometimes becomes folded into an irregular mass. Most of the amebas have a spherical or nearly spherical nucleus, especially the smaller species.

CHROMATIN

With respect to the arrangement of the chromatin in the living "resting" nucleus, four main types occur: 1, in a homogeneous mass in the form of a hollow or an apparently solid sphere or ovoid, with the nuclear membrane immediately outside of it or at some distance from it—*Cochliopodium*, *Hyalodiscus*, *Flabellula*, most *Thecamoeba*, *Endamoeba*—the majority of amebas belong to this group (fig. 2, a, b); 2, in large islands irregularly placed, immediately beneath the nuclear membrane, with or without a clearly distinguishable karyosome in or near the centre (fixing and staining often results in displacing the karyosome into excentric positions)—*Cochliopodium clarum*, *Rugipes bilzi*, *Karyamoebina*, *Metachaos annulata*, *M. gratum*, *Endamoeba nana* (fig. 2, c, d, f, g); 3, in two regularly formed polar caps—*Thecamoeba munda* (fig. 1, e); 4, in a layer of small grains of uniform size at a greater or less distance from the nuclear membrane—*Chaos diffluens* (*Amoeba proteus*), *Chaos chaos*, *Trichamoeba villosa*, *Metachaos discoides*, *Dinamoeba*, *Mayorella bigemma*, *Polychaos dubia* (fig. 1, h, i, j, k). In addition to these masses of chromatin there are found, after fixing and staining, other masses of stainable matter, usually irregularly placed, nearer the centre of the nucleus, and in some species "clouds" or concentric rings of fine dust-like stainable particles occur in the nucleus, whose chromatin constitution has not yet been fully established.

The number of nuclei in the trophic or vegetative stage of amebas varies. The great majority of species have a single nucleus; a considerable number have two nuclei (*Pelomyxa*, *Striolatus*); three species have about 15 nuclei (*Trichamoeba caerulea*, *Pelomyxa beleuskii*, *Flamella magnifica*); two species have from 50 to 80, each

(*Pelomyxa tertia*, *P. vivipara*); one species, possibly two, have about 125 (*Pontifex*) and three species have from 1000 to 2000 typically formed nuclei (*Chaos chaos*, *Metachaos laureata* and *Pelomyxa palustris*). In one species of ameba (*Astramoeba stella*) the nuclear membrane is single, of oblong shape, but the chromatin is in two masses, indicating probably a long pause in the telophase stage before complete division of the nucleus and of the cytoplasm, since binucleate amebas have never been observed in this species. The condition described is found in about 75 per cent of the amebas of this species. The binucleate condition generally may be explained as differing from the uninucleate only in the long delayed division of the cytoplasm.

CYTOPLASMIC DIVISION

This of course raises the question as to what factors cause cytoplasmic division if it is not the division of the nucleus. Although cytoplasmic division may be induced by a great majority of the nuclei of a multinucleate ameba dividing simultaneously, the considerable variations in number of nuclei observed in the multinucleate amebas indicate that the nuclei frequently divide independently of each other. It is significant too that a large majority of multinucleate amebas frequently become spread out in a thin sheet on the surface of the glass slide and for a longer or a shorter time are incapable of locomotion. While in this condition division frequently occurs in one species as the different marginal regions pull away from each other, and all but complete separation of the cytoplasm occurs in several other species. This phenomenon is very rare among the uninucleate amebas excepting a few of the very small species. There seems to be some connection therefore between the multinucleate condition and the tendency to spread out on the sur-

face, which in some species leads to division. It may be noted here also that the division which Roesel described and illustrated of "der kleine Proteus" is not

behavior, which may be regarded as additional evidence that Roesel had before him not one of the species designated *Amoeba proteus* by Leidy, but the much larger and

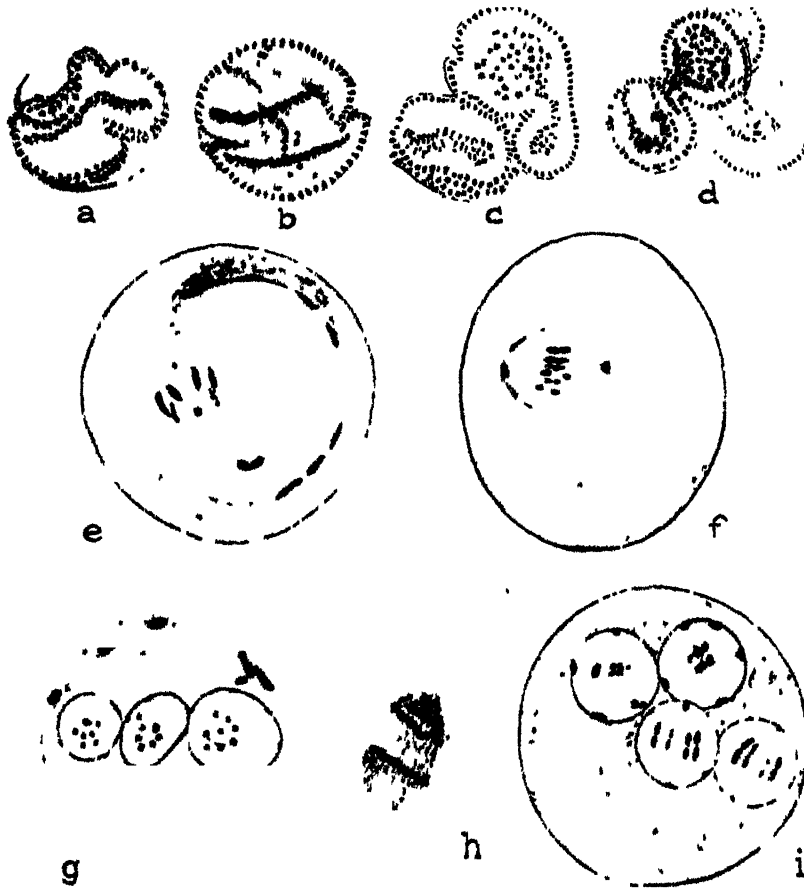


FIG. 3. NUCLEAR DIVISION IN THREE SPECIES OF AMEBAS

a, b, c, d, Chaos disfluens. *a*, vegetative divisions, chromatin grains dividing to form two layers, karyosome and membrane also dividing. *b*, complicated vegetative division leading, apparently, to four daughter nuclei. *c*, vegetative division, two daughter nuclei almost separated. *d*, vegetative division; four daughter nuclei almost separated. *e, f, g*, mitosis in cysts of *Councilmaniana muris*. *e*, nucleus in late prophase. *f*, upper chromosomes in metaphase, lower in early anaphase. *g*, three-nucleate cyst with diffuse karyosome and early stage of intradescmose in right-hand nucleus. *h*, mitosis in *Chaos disfluens* in (probably) a procystic stage, nucleus in anaphase. *i*, *Councilmaniana decumani*, four-nucleate cyst with two nuclei in metaphase. *a, b* (x660); *c, d* (x440), after Monica Taylor. *e, f, g, i* (x2500) after Kessel. *h*, after Doflein.

of the type observed in the common large uninucleate ameba but is more or less characteristic of multinucleate ameban

rarer multinucleate species which was subsequently rediscovered by H. V. Wilson in 1900.

MITOSIS

One of the most outstanding discoveries on the structure of the nucleus within the past decades has undoubtedly been due to the brilliant investigations of Kofoed and Swezy and their collaborators. They have been able by improved technique to establish a definite number of chromosomes for a number of parasitic amebas, which may very well prove to be the most definite characteristic for identifying these species. The importance of this discovery to parasitology can therefore be readily appreciated. But it is also of great scientific interest in that it furnishes the most definite knowledge we have of mitosis in the amebas, a process which was first discovered to occur in the amebas by Vahlkampff in 1904. Theretofore it was believed that amebas divided amitotically. One needs only to compare the figures of Kofoed and Swezy with those of Vahlkampff, which themselves marked an epoch in this field, to see what tremendous strides have been made in the knowledge of the ameban nucleus in 21 years. We now know that *Endamoeba coli* has 6 chromosomes, *E. dysenteriae* (*histolytica*) probably 6, *Karyamoebina falcata* about 20, *Councilmania muris*, 6 (fig. 3, e, f), *C. decumani*, 4 (fig. 3, i), *C. laflouri*, 8, (Kofoed, Swezy, Kessel).

This work on the nuclei of these amebas has also cleared up to a large extent other processes in mitosis, such as the origin of the centrosome from the karyosome, the central mass of deeply staining material in the nucleus; the origin and fate of the connecting strand between the centrosomes or intradesmose (Kofoed and Swezy, Kessel) a structure very similar to the centrodesmose in the metazoan cell but apparently more persistent (fig. 3, g); and the splitting of the chromosomes in metaphase. These phenomena are particularly well seen in *Councilmania muris* of rats and

mice, in the nuclei of which there is very little peripheral chromatin, almost no clouds of stainable material and in which the karyosome consists of a small number of discrete granules, two of which or the division products of one become the centrosomes. These conditions permit of almost diagrammatic pictures of the mitotic events, so sharply and clearly do these structures stand out. Incidentally it may be noted that the entire mitotic machinery is formed within the nuclear membrane, which must probably be taken to mean that the apparent extra-nuclear origin of the spindle of metazoan cells is a secondary development of the evolution of the mitotic process.

How different is the picture which the common ameba presents! Instead of but six clear cut granules enacting the simple mitotic drama on a perfectly clear stage, we have here several thousand chromatin grains, and a large and complicated karyosome going through a process of division apparently so complicated that it seems to bear only a remote resemblance to the traditional idea of mitosis (fig. 3, a, b, c, d). Each of the several thousand chromatin grains, arranged in a single layer underneath the nuclear membrane, divides during fission into two by a plane parallel to the surface of the nucleus, which in this species has a discoidal shape (fig. 3, a). The two layers of chromatin grains which result from this division then separate and at the same time the flat disk-shaped karyosome divides into two plates, apparently by a plane perpendicular to the short diameter of the karyosome. The outer layer of chromatin grains then sloughs off while one of the daughter karyosomes passes into it, the other karyosome remaining within the inner layer. Thus the two nuclei are formed during division according to the description by Monica Taylor ('24).

Although the main facts involved in this process of division may be definitely stated, the figures show that the process is very complicated and there is no convincing evidence of an actual mitotic process such as Doflein ('18) records (fig. 3, *b*). It must be pointed out however that Doflein fails to show definitely on what species of ameba he worked, and second, he certainly did not work on the vegetative division stages for he says most of his amebas were multinucleate (2 to 8), rounded up and persisted in this shape from one to four days (Schaeffer, '17). It is highly probable therefore that he worked on the shell-less cystlike stage or procysts of the common large ameba, which seem to be a substitute for the shell-bearing cysts of the parasitic species. And Doflein himself doubted whether the mitotic divisions he found represented the only way in which the nucleus of the ameba divided. We therefore still lack sufficient evidence to tell just how our common ameba divides during fission. It would be most extraordinary if after all the nucleus divided amitotically in this stage by means of some process resembling budding as has been suggested. Let us hope that investigations will speedily be initiated to settle this fascinating but tantalizing problem.

CHROMIDIA

The nuclear division processes constitute only a brief stage in the life cycle of the ameba, but we may use these processes as an introduction to the consideration of the other stages in the life cycle. Confining our discussion still to the common large ameba, we may proceed at once to the heart of the matter by asking: Do chromidia give rise to nuclei or do they not? Bott, Popoff, Carter, Ivanic and Monica Taylor ('24) speak affirmatively, and Kofoed ('23), on theoretical grounds,

believes the contrary. The origin of nuclei from chromidia has recently been described as follows (Monica Taylor, '24). Some of the several thousand chromatin grains arranged in a layer underneath the nuclear membrane, as described above, are shed into the cytoplasm through rupture of the nuclear membrane. Each grain of chromatin then divides until a cluster of about 8 grains are formed which is then considered as a new nucleus. The new nucleus appropriates some of the ameba's cytoplasm and soon thereafter forms a cyst wall about itself. The ameba becomes filled with hundreds of cysts of this kind (apparently not all of the chromatin grains develop into nuclei) and soon dies and disintegrates, freeing the cysts. The cysts hatch out as amebas and in order to grow to full size require the extraordinary long time of three or four months. Numerous illustrations are given by Taylor. Similar but very indefinite figures are also given by Hausman in a paper on the same subject. This is the affirmative side of the question.

The alternative explanation of the objective events just related is that the small organisms are parasites, as has been pointed out by several investigators. Neither the chromidial nor the parasite hypothesis has however been actually proved. Since the burden of proof in science rests upon him who makes an assertion, no final statement is admissible on this subject unless accompanied by clear proof. The solution of this problem for those who hold the chromidial hypothesis, requires at least the unmistakable identification, as determined by observation, not by deduction, of the chromatin grains with the beginning stage of the small organisms; and second, an isolation pedigree culture of one of these organisms until absolute identity with the parent organism as to details of structure is es-

tablished. It would be more practical perhaps to settle the second point first. Those who hold to the parasite hypothesis must be able to furnish proof by re-infecting other amebas with the supposed parasite. The figures thus far published on these putative young amebas do not convincingly resemble the adult "mother" ameba from which they came. It is only fair to say that Monica Taylor is one of those who recognizes this and is at work in an earnest endeavor to solve this vexatious question.

If we adopt then the critical scientific attitude we find no proof that the life cycle of the common large ameba includes more than the irreducible minimum, namely, reproduction by fission. That is all. Fission may be mitotic or amitotic; we do not know definitely because the various authors did not use pure cultures and most of them did not make it clear which one of three to five possible species were employed. The same statement applies to the accounts of sporulation and encystment.

FLAGELLATE STAGES

Other species of amebas however have more complicated life cycles, as is well known. Thus in the parasitic species reproduction occurs in the encysted stage resulting frequently in 16 small amebas and in other species living in the soil or in cultures of feces outside of the body, a flagellate stage may often be observed. The most interesting case of the latter kind has to do with *Tetramitus*, a flagellate from the feces of the rat, which was described by Perty in 1852. This flagellate of rather complicated structure was found recently to have an ameboid stage in its life cycle. An ameba of typical form hatches out of a cyst. It feeds and divides to form other amebas for a number of generations. Some of these encyst.

Others become transformed directly into the traditional flagellate *Tetramitus*. In this stage growth occurs followed by repeated divisions. Sooner or later the flagellates transform directly into amebas which after a time encyst, completing what is known of the cycle. This extremely interesting change from an ameba into a flagellate of rather complicated structure and back again is one of many indications that the amebas and the flagellates are very closely related.

GENETICS

In the field of genetics regrettably little has been done with amebas. Isolation pedigree cultures have been employed to test the specific characters of several amebas and, by means of simple statistical methods, the existence of five races has been indicated in *Endamoeba histolytica* (*dysenteriae*) and four in *E. coli* (Dobell and Jepps). By means of isolation pedigree cultures it has also been found that there are rhythms in the rate of fission in *Mayorella* (*Amoeba*) *bigemma* comparable to those found in the infusoria, but whether they are of the same nature fundamentally has not been determined. The rate of fission in five species pedigreed singly is extremely irregular varying from two to three divisions in 24 hours to one division in 8 to 12 days, at room temperature. The cause of this irregularity is not known (Schaeffer, Botsford).

REGENERATION

The question of regeneration in ameba has received a great deal of attention in the past. After it was established however that the enucleated part of a bisected ameba died after 10 or more days while the nucleated part lived, little was done in this field until very recently. A quarter to a third was cut off an ameba almost daily to see what the effect would be on sub-

sequent reproduction. After a series of such excisions were made, extending over a month, during which time the ameba did not divide, further excisions were discontinued whereupon the ameba grew in size and divided normally. Since it had been shown before that the common large ameba usually dies if it does not divide in 9 days, it seems that excisions are in some way a substitute for divisions (Hartman, Phelps). The interesting observation was also made that of two daughter amebas from the same mother, the one bisected as above indicated and the other allowed to divide normally, the normal one produced five times as much protoplasm as the bisected one. It was found too, that the "minimal reorganization mass," the smallest piece capable of regeneration, was at last as small as $1/80$ of the ameba, being therefore the smallest regenerating mass yet recorded among the protozoa (Phelps).

AMEBOID MOVEMENT

In the foregoing paragraphs are described some of the more recent published researches bearing more or less directly upon the morphology of the amebas, but including also a number of physiological discoveries arising out of these researches. It now remains to consider the results of some investigations on amebas, whose primary object was physiological. For the purpose of general discussion these researches may be divided into two groups: 1, those dealing with ameboid movement and 2, those dealing more particularly with the reactions of amebas toward various stimuli.

Speaking first of ameboid movement, it may be pointed out that the universal interest which this phenomenon excites among biologists is attested by the large number of theories of ameboid movement which have been published. But although these theories reflected interest in

the subject, it seems that they did not add to an understanding of it. Just as the 260 or more theories of sex quietly passed into oblivion when the work of Mendel became known, so the theories of ameboid movement are being forgotten as the results of observation and experiment on the movement of amebas are accumulating. We do not therefore think it profitable to discuss any of these theories here, but shall instead devote the available space to objective data which have been rapidly accumulating in the past few years.

The activities of the surface layer of the ameba, that is, the plasma membrane have already been described. Judging from the observations on its behavior, this layer is the surface tension layer and the question arises here whether it is a necessary factor in ameboid movement. Since it does not move in the same way in the pseudopods of *Diffugia* or of foraminifera and is of course absent as a moving layer in ciliates and those plant cells where streaming protoplasm occurs, its movement as seen in the amebas probably does not constitute an essential factor in ameboid movement. But its movements nevertheless indicate that the surface tension is greater at the anterior ends of active pseudopods than over the rest of the ameba, and this fact if correctly interpreted, may prove to be a useful guide in further experimental analysis.

The discovery that amebas move in wavy or sinusoidal paths when comparatively free from external stimulation in clear culture fluid, is of considerable interest because of the probability that this path is a projection of the well known helical spiral paths of ciliates and flagellates on a plane surface, the ameba being of course, restricted in its movements to two dimensions of space (fig. 4). This probability is strengthened by the fact that the flagellate

stages of those amebas which go through these stages move in helical spirals. It has been found also that a great many other organisms, such as the larvae of many species of aquatic invertebrates and all motile spermatozoa move in similar paths. In fact all animals including man and all motile plants move in spirals of some form when the orienting senses are not functioning (Schaeffer, '20). Very little of the nature of this fundamental mechanism affecting movement has been learned excepting that in the ciliates, where an extensive investigation covering 165 species showed, (1) high correlation between the direction of the spiral, whether right handed or left handed, and generic characteristics, that is, the species of most of the genera containing two or more species swim, all either right handed or left handed; (2) the investigation showed no correlation whatever between any visible morphological structures and direction of turning (Bullington). Because of its universal occurrence and the absence of correlation to visible structure, this spiralizing tendency is difficult to investigate experimentally by analytical methods. It appears to be controlled by the spatial aspect of some feature of the locomotive machinery, but with such an enormous variety of locomotive apparatus as is comprised under all the motile animals and plants, it is quite evident that one must go behind visible morphology to stereochemical aspects of the protoplasm, for a cause, at least of the difference between left hand and right hand turning.

Ameboid movement as generally thought of is restricted to those form changes of protoplasm which are due to the streaming of the protoplasm, and as thus conceived the heart of the problem is to discover what causes protoplasmic streaming. All other phenomena associated more or less frequently with stream-

ing, such as the formation of ectoplasm and the conversion of it into endoplasm, are accessory and nonessential, for in some organisms where streaming occurs there is no regular formation of ectoplasm, e.g., plant cells and foraminifera. For practical purposes, however one must confine one's experimental work to one or at most a few forms, and for this reason it becomes necessary and often very desirable to study the accessory phenomena, because these phenomena often are a measure of the streaming activity and serve

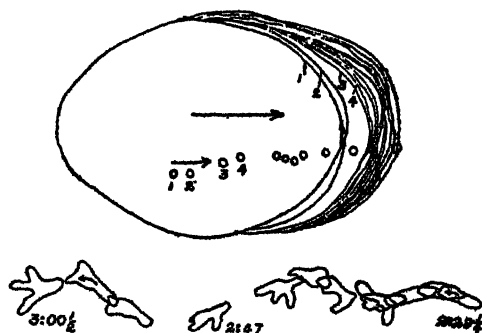


FIG. 4. Above, *Thecamoeba sphaeronucleosus*

Showing movement of the plasma membrane as indicated by a small particle attached to it. Twelve successive outlines of anterior end of ameba are shown, corresponding with 12 successive positions of the particle. The plasma membrane moved over 3.5 times as fast as the ameba. Below, waves in a 30-minute section of path of *Metachaos discoides*.

therefore as a guide in its experimental analysis. But it is nevertheless true that the great interest displayed in ameboid movement is due to its very widespread occurrence in animals and plants, and that the only constituent phenomenon that one can see which is common to all cases of ameboid movement wherever it is found, is streaming.

A number of researches have been recorded in the past few years which, it may be presumed, were directed upon this central problem of ameboid movement. Of these, the investigations of Pantin seem

to have been particularly well planned for they have yielded clear cut and important information on this subject. The work was done on marine amebas which, because of the medium in which they live, offer certain decided advantages over fresh-water species for certain purposes. One of the very interesting conclusions from this work is that there is a rise in hydrogen ion concentration in an active pseudopod. This was determined by using neutral red as an intra vitam stain.

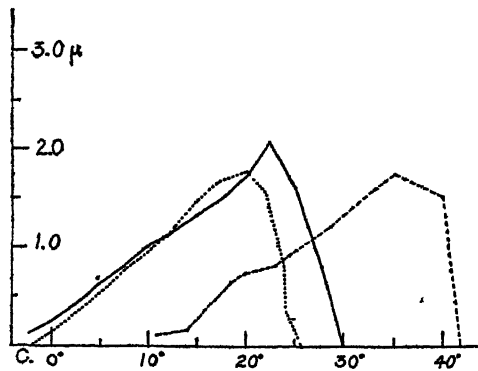


FIG. 5. CURVES ILLUSTRATING THE EFFECT OF TEMPERATURE ON VELOCITY OF THREE SPECIES OF AMEBA

Solid line, "Type A" (*Trichamoeba gumia*?) ameba, after Pantin; dotted line, "type B" ameba, after Pantin; broken line, *Cochliopodium* sp. (velocity multiplied by 1.6. Schaeffer, '24). Note the very suggestive general identity of the high optimum curve of *Cochliopodium* with the other two curves.

It could not be ascertained with certainty, however, whether only the small granules or the fluid cytoplasm, or both, became more strongly acid. By immersing the amebas in various acid solutions it was found that hydrochloric, acetic, butyric, lactic, sulphuric and oxalic acids inhibited ameboid movement, each at about the same rate as shown by the plotted curves. But citric and tartaric were much less effective in inhibiting movement. In these solutions the paralysis point ranged from pH 5 to pH 6, while in the first

series of acids the paralysis point was about pH 7. The inhibiting effect seems to be due to the pH concentration, but the protective effect of the citrate and the tartrate remains unexplained.

The effect of temperature on velocity of movement on the same two species of ameba showed the optimum temperature for one species to be from 22°C. to 25°C., and for the other species 20°C. (Pantin) (fig. 5). These optima, it may be remarked, were probably fixed by the temperature of the medium in which they grew, for the optimum temperature as measured by the rate of movement of an ameba living in shallow tidal pools at Tortugas, Florida, in which the temperature rises to 40°C. daily in the sun, is 35°C. or slightly above. The optimum for this ameba is in fact 50 above the death point of the amebas Pantin employed (Schaeffer) (fig. 5). When the rate of movement in various temperatures is plotted against the temperature, the resulting curve to the optimum is almost a linear function of the centigrade temperature and is closely similar to the temperature-velocity curves of many other biological processes, particularly protoplasmic streaming in plant cells and the leucocytes of human blood (Pantin, Schaeffer, Kanitz, McCutcheon).

After the optimum temperature is reached in these amebas, the curve drops rapidly to the base line, an effect which may be due to the destruction of some substance concerned in locomotion. In fact this apparently destructive effect is already present to a slight degree before the optimum is reached, because if the velocity of an ameba is measured at 10°C., for example, and then at 20°C., and then again at 10°C., the velocity is less on reentering 10°C. Nevertheless within a fraction of an hour the ameba regenerates the substance destroyed and recovers its original velocity.

On the other hand observation indicates that several, perhaps all species of amebas can be acclimated to higher optimum temperatures, which would mean that substances are gradually built up in much the same way that the substance mentioned above was regenerated, but at the same time containing within them the possibility of a destructive effect due to the temperatures near the optimum. Herein are opportunities for whole series of important quantitative experiments on the nature of ameboid movement which would also undoubtedly shed light on other biological processes.

The treatment of amebas with solutions of various chemicals in order to learn something of the nature of ameboid movement, has been carried on by a number of observers in the past few decades. Similar experiments have also been made upon leucocytes of man and other animals for the same purpose. Studies of this sort upon the common large ameba have shown that all chemical solutions thus far accurately tested have had the effect of slowing down the rate of movement, if indeed any effect was detectible at all. This is an extraordinary result, but it is of course only a "progress report," and the final statement on the subject may be different. In recent work (Edwards, Forgrave) with the solutions of the chlorides of sodium, lithium, potassium, etc., it was found that the rate of locomotion of ameba when immersed in them is slowed down in a degree depending upon the cation, the concentration of the solution and the time of immersion. The rate of movement was greatest in solutions of sodium chloride. Acid solutions cause the surface to become sticky in dilutions up to $N/20,000$. Bases (sodium and potassium hydroxide) on the other hand seem to liquefy the surface protoplasm and make it susceptible to rupture.

One of the interesting results of this work with chemicals is the action of weak ($N/300$) solutions of the chlorides of sodium, calcium, lithium, potassium, in causing the formation of food cups in ameba. This is the only case known in ameba where a completely generalized stimulus sets into operation what seems to be a comparatively highly specialized "racial habit," which ordinarily is initiated only by localized stimuli (Edwards).

It is interesting to note here that various species of marine amebas representing 3 different families move much more rapidly in dilute sea water than in normal sea water, and a similar effect was noted in a few marine ciliates. These amebas live only in the sea, so far as known, and one of them is unable to live in fresh water for even a few minutes. These amebas have presumably lived for a long time in the sea and yet they have been unable to overcome the inhibiting effect of the salts in the sea water. This indicates the presence of an unalterable relationship between these salts and an essential reaction involved in ameboid movement and probably also in ciliary contraction (Schaeffer, '24).

BEHAVIOR

In proportion to the total amount of research on amebas, comparatively little has been done in the field of behavior within the past few years. One series of experiments directed upon the ability of the ameba (species not mentioned) to modify its responses has shown that this is possible although the conclusion is somewhat indefinite and the response is of a negative nature, not a positive one. Most of the amebas used in the experiment were negative to large areas of very intense light. It was found that there is a decrease in the number of attempts to continue in the original direction (into the light) as the number of trials increases.

The ameba "learns" to avoid the light (Mast and Pusch).

Another series of experiments on the effect of light on ameba with reference especially to the latent period, reaction time, etc., has shown that in general the ameba reacts substantially like other organisms. The ameba responds to a sudden increase of illumination after a few seconds by a cessation of movement, and this intervening period of time is here known as the reaction time. It is found that the reaction time varies inversely with the intensity of the light. Only a momentary flash of light is needed to inhibit streaming some seconds later. The length of time the light shines is therefore the stimulation period, and the time between the end of the flash and the inhibition of movement is the latent period. The latent period, like the reaction time, varies with the intensity of the light, being short in strong light and lengthening with decreased intensity of light. It was found also that from one to two minutes must elapse after sudden illumination before a second response could be obtained. Mechanical shocks produce effects substantially like the stimuli from light, from which the conclusion is drawn that the effect of light is not necessarily due to the presence of a photo-chemical substance. Perhaps the most unlooked-for result of this work is the absence of any temperature effect on the reaction time. It is however not impossible that the temperature effect may be small and may have remained hidden under the individual variations, which were not inconsiderable (Folger).

In the first of several proposed papers Schwitalla has recorded a large number of detailed observations on the effect of temperature on the movement of *Metachaos discoides* and on the common large ameba as measured by the movement of

the posterior end. He records the occurrence of irregular rhythms in the velocity, the cause of which however was not detected. The rhythms of fast and slow movement changed somewhat as the temperature changed, that is, as the temperature increased from 15°C. to 25°C. the fast rhythms became fewer or shorter or both, as compared with the slow rhythms.

Beers records a very interesting case of the common large ameba feeding on the large ciliate *Frontonia leucas*, by pinching it into two, as occasionally happens also with paramecium and blue stentors. Why the ameba should not ingest the whole frontonia or paramecium is hard to see, for much larger food objects are frequently eaten. This raises the question whether the ameba actually pinches the ciliate into two as has so often been assumed. It is more probable that the ciliates constrict themselves when the food cup of the ameba presses lightly against their cilia, as they are often seen to do when threading their way through debris. The body of the ciliate at the point of constriction under these conditions is always smaller than the hole or slit in the debris, so that the animal can readily rotate on its long axis. A time element is of course involved, and the ameba closes in upon the prey slowly enough for such a constricting process by the ciliate to occur. It cannot be accepted without actual proof, therefore, that the ameba actually expends the necessary energy required to cut the ciliate into two instantly. These observations have often been assumed to be particularly fatal to the simple surface tension theory of ameboid movement, but the critical attitude suggested above need occasion no fears as to its possible resurrection, for this theory was already sufficiently dead.

LITERATURE LIST

(Starred references contain extensive bibliographies)

- BEERS, C. D. 1924. Observations on amoeba feeding on the ciliate *Frontonia*. Brit. Jour. Exp. Biol., Vol. 1, pp. 335-341. 2 figs.
- *BOECK, W. C., AND C. W. STILES. 1923. Studies on various intestinal parasites (especially amoebae) of man. U. S. Pub. Health Bull. No. 133, pp. xxvi + 202. 80 figs.
- BOTSFORD, E. F. 1922. Rhythms in the rate of reproduction of *Amoeba bigemma*. Proc. Soc. Exp. Biol. Med., Vol. 19, p. 397.
- *BULLINGTON, W. E. 1925. A study of spiral movement in the ciliate infusoria. Arch. f. Protistenk., Vol. 50, pp. 219-274.
- BUNTING, M. 1922. A preliminary note on *Tetramitus*, a stage in the life cycle of a coprozoic amoeba. Proc. Nat. Acad. Sci., Vol. 8, pp. 294-300.
- CARTER, L. A. 1919. Some observations on *Amoeba proteus*. Proc. Royal Phys. Soc. Edinburgh, Vol. 20, pp. 193-211. 1 fig.
- *CASE, J., AND J. HOPKINSON. 1905. The British Fresh-Water Rhizopoda and Heliozoa. Vol. 1, Ray Society. 150 pp., 16 pls.
- CHAMBERS, R. 1920. Dissection studies of amoeba. Proc. Soc. Exp. Biol. Med., Vol. 18, p. 66.
- CHAMBERS, R. 1921. The effect of experimentally induced changes in the consistency on protoplasmic movement. Proc. Soc. Exp. Biol. Med., Vol. 19, p. 87.
- CROZIER, W. J., AND H. FEDERIGHI. 1924. Critical thermal increment for the movement of oscillatoria. Jour. Gen. Physiol., Vol. 7, pp. 137-150. 6 figs.
- DE HAAN, J. 1922. Mobilite amiboide et phagocytose. Arch. Neerlandaises de Physiol., Vol. 6, p. 388.
- DOBELL, C., AND M. W. JEPPE. 1918. A study of the diverse races of *Entamoeba histolytica* distinguishable from one another by the dimensions of their cysts. Parasitol., Vol. 10, pp. 320-351. 7 figs. 1 pl.
- *DOBELL, C. 1919. The amoebae living in man. vi + 155 pages. London.
- DOEFLIN, F. 1918. Die vegetative Fortpflanzung von *Amoeba proteus* Pallas. Zool. Anz., Vol. 59, pp. 257-268. 12 figs.
- EDWARDS, J. G., AND H. S. FORGRAVE, JR. 1923. The rate of locomotion of amoeba in alkali chlorides. Johns Hopkins Hosp. Bull., Vol. 34, pp. 387-389.
- EDWARDS, J. G. 1924. The action of certain reagents on amoeboid movement. Brit. Jour. Exp. Biol., Vol. 1, pp. 571-595. 1 pl.
- EDWARDS, J. G. 1925. Formation of food-cups in amoeba induced by chemicals. Biol. Bull., Vol. 48, pp. 236-239. 4 figs.
- FOLGER, H. T. 1925. A quantitative study of reactions to light in amoeba. Jour. Exp. Zool., Vol. 41, pp. 261-291. 3 figs.
- FÜRTH, O. 1922. Zur Theorie der Amöboiden Bewegung. Arch. Neerlandaises de Physiol., Vol. 7, p. 39.
- GALTSOFF, P. S. 1923. The amoeboid movement of dissociated sponge cells. Biol. Bull., Vol. 45, pp. 153-161. 1 fig.
- GIERSBERG, H. 1922. Untersuchungen zum Plasma-bau der Amöben, im Hinblick auf die Waben-theorie. Arch. f. Entw.-Mech., Vol. 51, pp. 150-250.
- GOODRICH, H. B. 1924. Cell behavior in tissue cultures. Biol. Bull., Vol. 46, pp. 252-262. 9 figs.
- GRAY, J. 1922. The mechanism of ciliary movement. Proc. Royal Soc., B., Vol. 93, p. 122.
- GRAY, J. 1923. The mechanism of ciliary movement. Proc. Royal Soc., B., Vol. 95, p. 6.
- HABERLANDT, L. 1919. Ueber Amöboiden Bewegung. Zeitschr. f. Biol., Vol. 69, pp. 409-436.
- HARTMANN, M. 1924. Der Ersatz der Fortpflanzung von Amöben durch fortgesetzten Regenerationen. Arch. f. Protistenk., Vol. 49, pp. 447-464.
- HAUSMAN, L. A. 1920. A contribution to the life history of *Amoeba proteus* Leidy. Biol. Bull., Vol. 38, pp. 340-352. 2 pls.
- HAYES, CARMELA. 1924. Nutritive spheres in amoeba. Quart. Jour. Micros. Sci., Vol. 69, pp. 144-149.
- HEGNER, R. W. 1920. The relations between nuclear number, chromatin mass, cytoplasmic mass and shell characteristics in four species of the genus *Amoeba*. Jour. Exp. Zool., Vol. 30, pp. 1-95.
- HEILBRUNN, L. V. 1921. Protoplasmic viscosity changes during mitosis. Jour. Exp. Zool., Vol. 34, pp. 417-447.
- HOOVER, M. J. 1922. A comparison of an amoeba, *Vahlkampfia patuxenti* with tissue culture cells. Jour. Exp. Zool., Vol. 35, pp. 1-11.
- HOOVER, M. J. 1923. Contractile vacuoles in amoebae-factors influencing their formation and rate of contraction. Jour. Elisha Mitchell Sci. Soc., Vol. 39, pp. 6.
- HOWLAND, R. 1924. Dissection of the pellicle of *Amoeba verrucosa*. Jour. Exp. Zool., Vol. 40, pp. 263-270. 15 figs.

- HOWLAND, R. 1924. Experiments on the contractile vacuole of *Amoeba verrucosa* and *Paramecium caudatum*. Jour. Exp. Zool., Vol. 40, pp. 251-262. 7 figs.
- HYMAN, L. H. 1917. Metabolic gradients in amoeba and their relation to the mechanism of amoeboid movement. Jour. Exp. Zool., Vol. 24, pp. 55-99. 14 figs.
- IVANIC, M. 1924. Zur Kenntniss der Fortpflanzungserscheinungen einiger Süßwasseramöben. Arch. f. Protistenk., Vol. 50, pp. 113-134. 24 figs.
- *JENNINGS, H. S. 1920. Life and death, heredity and evolution in unicellular organisms. 233 pages. 53 figs.
- KEPNER, W. A., AND W. H. TALLIAFERRO. 1917. Food-reactions of *Pelomyxa carolinensis* Wilson. Jour. Exp. Zool., Vol. 24, pp. 381-394.
- KESSEL, J. F. 1924. The distinguishing characteristics of the parasitic amoebae of culture rats and mice. Univ. Cal. Pub. Zool., Vol. 20, pp. 489-544. 3 figs., 6 pls.
- KOFOID, C. A. 1923. The life cycle of the protozoa. Science, N. S., Vol. 57, pp. 397-408.
- KOFOID, C. A., AND O. SWEZY. 1924. *Karyamoeba falcata*, a new amoeba from the human intestinal tract. Univ. Cal. Pub. Zool., Vol. 26, pp. 221-242. 2 figs., 2 pls.
- LAPAGE, G. 1922. Cannibalism in *Amoeba vespertilio*. Quart. Jour. Micros. Sci., Vol. 66, pp. 669-710. 3 figs., 2 pls.
- LOEB, L. 1921. Amoeboid movement, tissue formation and consistency of protoplasm. Amer. Jour. Physiol., Vol. 56, pp. 140-167.
- MAST, S. O. 1923. Mechanics of locomotion in amoeba. Proc. Nat. Acad. Sci., Vol. 9, pp. 258-261.
- MAST, S. O., AND L. C. PUSCH. 1924. Modification of response in amoeba. Biol. Bull., Vol. 46, pp. 55-59. 1 fig.
- MCCUTCHEON, M. 1923. Studies on the locomotion of leucocytes, II. Amer. Jour. Physiol., Vol. 66, p. 185.
- *NÖLLER, W. 1922. Die wichtigste parasitischen Protozoen des Menschen und der Tiere. I, die parasitischen Rhizopoden. 272 pp. Berlin.
- *PANTIN, C. F. A. 1923. On the physiology of amoeboid movement. Jour. Marine Biol. Ass. United Kingdom, Vol. 13, pp. 24-69. 10 figs.
- PANTIN, C. F. A. 1924. On the physiology of amoeboid movement. II. Brit. Jour. Exp. Biol., Vol. 1, pp. 519-538. 4 figs.
- PHILIPS, L. A. 1925. Experimental analysis of factors concerned in division in amoeba. Anat. Record, Vol. 31, p. 312.
- REYNOLDS, B. D. 1924. Interactions of protoplasmic masses in relation to the study of heredity and environment in *Arcella polyzona*. Biol. Bull., Vol. 46, pp. 106-140.
- *SCHAEFFER, A. A. 1920. Amoeboid movement. vii + 156 pages. Princeton press.
- *SCHAEFFER, A. A. 1926. The taxonomy of the amoebas with descriptions of thirty-nine new marine and fresh-water species. Publ. Carnegie Institution of Wash., No. 345 (contains full bibliography of previous papers by this author).
- SCHWITALLA, A. M. 1924. The influence of temperature in the rate of locomotion in amoeba. Jour. Exp. Zool., Vol. 39, pp. 465-513. 8 figs.
- SWEZY, O. 1922. Mitosis in the encysted stages of *Endamoeba coli*. Univ. Cal. Pub. Zool., Vol. 20, pp. 313-322. 2 pls.
- TALLIAFERRO, W. H., AND F. O. HOLMES. 1924. *Endamoeba barresi* n. sp. from the turtle, *Chelydra serpentina*. Amer. Jour. Hygiene, Vol. 4, pp. 155-168. 1 pl.
- TAYLOR, MONICA. 1918. Note on the collection and culture of *Amoeba proteus* for class purposes. Proc. Royal Soc. Edinburgh, Vol. 20, pp. 179-182.
- TAYLOR, MONICA. 1923. Nuclear divisions in *Amoeba proteus*. Quart. Jour. Micros. Sci., Vol. 67.
- TAYLOR, MONICA. 1924. *Amoeba proteus*: Some new observations on its nucleus, life history and culture. Quart. Jour. Micros. Sci., Vol. 69, pp. 119-143. 10 figs.
- WAGNER, E. H. 1924. A precipitin test in experimental amoebic dysentery in cats. Univ. Cal. Pub. Zool., Vol. 26, pp. 15-20. 1 pl.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of particular significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

CUÉNOT ON ADAPTATION

By John H Gerould, Dartmouth College

The French have been characteristically strong and even brilliant as encyclopedists. The assembling, summarizing and interpreting to the general reader of results of research by specialists in every field of science, though no longer within the power of a single writer, is now accomplished with considerable success by such an organization as that constructed by Dr. Toulouse, Director of the *École des Hautes Études*, who for his *Encyclopédie Scientifique* divides science and its applications to medicine, education, industry, engineering, etc., into about thirty-four departments, each under the direction of a competent leader who selects specialists with breadth of view and power of popular expression to interpret to the public the results of science in their respective fields by means of handbooks of convenient size (usually about 300 or 400 pages).

Professor Maurice Caullery has been happily chosen as Director of the Department of General Biology and has himself contributed to the series a work on "*Le Parasitisme et la Symbiose*." The fifth independent volume in the field of general biology is "*L'Adaptation*" (G. Doin, Paris, 1925, pp. 420) from the pen of Professor L. Cuénot of Nancy, already well known to the scientific public by his "*La Genèse des Espèces Animales*" and other important works.

Cuénot has approached the questions of how and why organisms are fitted to their environment not only from the standpoint and with the training of a critical biologist but also with the liberal spirit of a broad and open-minded philosopher.

In defining the subject, distinction is made between modifications ("*accommodats*") or somations, which an individual plant or animal acquires in an environment new to it, corresponding to the changes of acclimatization experienced by a group of individuals and their offspring when introduced into a country new to them, and, on the other hand, hereditary, or "statistical," adaptations. "Statistical" is a term applied to adaptations to a given condition or medium, which are numerically frequent, but not necessarily always present, under such conditions. The webbed foot characteristic of aquatic animals, fleshy leaves of plants of desert or seaboard, dwarf plants of mountain tops, are chiefly under hereditary control and statistically numerous, though not universally found, under these given conditions; that is, not all aquatic vertebrates have webbed feet.

Among plants, especially, it is difficult to distinguish by mere inspection between modifications ("*accommodats*"), which disappear when the seed of the somatically modified plant is sown under normal environment, and hereditary or "statistical" variations. Among animals, usually less subject to environmental influences, "sta-

tistical" or hereditary variations are not so often combined with non-hereditary modifications.

It is very unfortunate in the opinion of the reviewer that this excellent book is marred by the constant use of this confusing and inappropriate term "statistical," as applied to hereditary variations and adaptations. The relative abundance, or statistical feature of hereditary adaptations is a minor matter of doubtful significance. It does not even distinguish such adaptations from modifications ("accommodations"), for the latter are also facultative and not universal under a given set of circumstances. The term "ethological" which Cuénot suggests as synonym of "statistical" is likewise equivocal and confusing, for modifications or accommodations are also distinctly ethological. It is difficult to find a term characterizing such adaptations as stable and subject chiefly to the control of hereditary factors without using the word "hereditary." "Stable" may be used, if one has occasion to avoid the use of "hereditary," but not "statistical." "Hereditary" is itself not free from objections, but it is clear and sufficiently distinctive.

The author properly emphasizes the fact, which Weismann and other extreme selectionists have passed over lightly, that many organs are nearly or quite useless. As examples, he calls to mind vestigial structures which have ceased to function and also organs which are greatly overgrown (hypertelic) and an encumbrance, such as the splendid plumage of certain male pheasants and birds of Paradise which is so enormous as to make flight impossible, the excessively long horns of the eland, the canines of the sabre-toothed tiger, the grotesquely large thoracic appendages of certain Brazilian leaf hoppers. Moreover certain other organs, internal or external, are useful but not

necessary, like the spleen, the uropygeal gland (lacking in certain birds), the air-bladder of fishes the presence or absence of which is evidently a matter of small importance. Cuénot has proved experimentally that amputation of the breathing tube of the water bug, *Nepa*, and the prominent spur upon the femur of the middle pair of legs in the backswimmer, *Notonecta*, the latter supposedly useful for cleaning the mouthparts, interferes in no perceptible way with either insect's activities and functions. The fact that useless or nearly useless organs are sometimes produced leads to an inquiry as to how variations occur, whether at random or in definite directions, fortuitously or orthogenetically.

Cuénot discusses orthogenesis, the type of variation familiar to paleontologists as the tendency of an organ or combination of organs to vary progressively from one geological period to the next, as if tending toward a definite end, e.g., the classic example of the evolution of the hoof from a single toe in the succession of extinct ancestors of the modern horse. Orthogenesis is recognized as a real method of evolution, independent of both natural selection and environmental action. Just as, in the growth of the individual, a mass of unformed tissue shapes itself under unknown internal control into an organ adapted to perform a definite function, so in the history of the race an organ which is at first unformed and useless may acquire a function or may change its function. Orthogenesis signifies then a series of evolutionary changes seemingly directed toward a definite end. In this category the author places the acquirement of a fixed, internally regulated, bodily temperature by the higher vertebrates, the evolution of mammary glands from simple cutaneous glands, the feathers of birds, originating by degrees

from reptilian scales, the electric battery of *Torpedo* transformed from masses of muscle upon the upper jaw, the wing of bat, bird or insect. "It all takes place as if directed toward an end, as if the beginning foreshadowed the conclusion."

Of the three theories which have been advanced to explain the evolution of adaptations: Lamarckianism, Darwinism (or natural selection), and the mutation theory, the last naturally receives the most extensive treatment.

"Darwinism, comprising Lamarckianism by inclusion, is therefore a theory of general application, and its immense success is easily understood; its logic is irresistible: the occurrence of inheritable variations cannot be denied; the tendency toward an indefinite increase in the number of species is certain; and also the destruction of an enormous number of individuals; the conclusion which seems inevitable is the survival of the better adapted, continuous progress, the extension and diversification of life." But while artificial selection involves intelligent choice in the destruction of superfluous individuals, natural selection, in the author's opinion, is nonselective. It involves destruction but not construction.

The discussion of the mutation theory includes a brief critique of recent experiments bearing on the inheritance of acquired characters, all of which are inconclusive. The author denies formally and completely the inheritance of acquired characters, because "it is necessary to have a firm opinion."

Mutations arising in a state of nature vary in natural vigor. They may be (1) lethal and disappear at once or exist only in a latent, compensated state, (2) less viable than the type and gradually disappear (e.g. albinos, mammals with pendant ears), (3) equally viable, and so

coexist with the type, thus constituting a polymorphic species, or (4) more vigorous than the type, like the melanic mutation of the peppered moth, tending to supplant.

The occupation of any newly established environment from which former inhabitants, if any, have disappeared is due, Cuénot points out, to the filtering in, from neighboring regions, of species already *preadapted* to the new environment. Thus by trial and error organisms adapt themselves to new regions. To survive, they must already be sufficiently adapted both as to instincts and to structure.

The success of a species arising by mutation in establishing itself depends upon "differential fertility," the two elements of which are the number of eggs laid and the death rate. Cuénot gives a formula for the annual loss of individuals in a race numerically constant, based directly upon the number of eggs produced by a single female and inversely upon the death rate.

To a Darwinian selectionist differential mortality means the survival of the fit and continuous progress by constructive selection; to the mutationist differential mortality means the elimination of the weak and abnormal, the maintenance of a healthy mediocrity; moreover mortality to a large extent is non-selective, the strong and the weak, the adapted and the non-adapted, being indiscriminately eliminated.

The study of orthogenetic series in paleontological succession shows that mutation may result sometimes in organs which are disproportionately large and cumbersome or sometimes completely atrophied. Alternation occurs between periods of mutation and of establishment of mutants as species. Certain points in the organism are more plastic than others, more subject to orthogenetic change. In the main, the changes are small and gradual; others necessarily involve a

profound structural and physiological alteration affecting the whole body, as when a left-handed type of snail give rise to right-handed descendants, no intermediate condition being possible. Rarely does nature make use of large, abrupt variations such as those which under artificial selection have produced, for example, the bull-dog, the ancon sheep, the rumpless fowl. On the contrary variation occurs by "gradual changes affecting in succession different organs, the coördination of which constitutes the adaptation to the environment."

Denying the explanations of adaptive evolutionary change advanced by Lamarck and Darwin, viz.; the inheritance of acquired characters and natural selection, the mutation theory has nothing to offer as a substitute. Cuénot acknowledges the need of discovering some new principle, or factor, internal or external, capable of controlling variations and directing them toward a definite end. This need is especially felt in studying such complex organs as the eye or the ornamentation of organs of such rare and useless beauty as the feathers of the peacock or *Argus* pheasant. Simply stated, we need to know how growth is controlled and differentiation determined.

In Part Three Cuénot interestingly describes many concrete cases of adaptation, the underlying principles of which have already been stated. The conclusion is reached that non-inherited modifications tend to be associated with hereditary variations of similar nature. Thus one may find on a mountain-top plants of a given species which owe their adaptation in various degrees to hereditary and to environmental factors; some are in the condition of non-hereditary modifications and would revert to the lowland type when removed to the plains; others are hereditarily fixed and would not thus respond.

Finally Cuénot discusses the metaphysics of the stupendous problem of adaptation, distinguishing between the mechanical or "efficient" cause, or how adaptations have originated, and their purpose, or why they have come to exist. Teleological concepts can be properly applied only to man's own instruments and machines. It is absurd to assign a final cause (ultimate purpose) to a phenomenon like the rainbow or sunlight clearly independent of mankind. Not less so is the application of such concepts to most organic phenomena.

But organs have useful functions. They are, in a sense, purposeful; and this usefulness of organs, individuals, or species, is only a fragment of a larger usefulness which includes all living things, because, though individuals die, life as a whole flows on. The ultimate biological adaptation is the conservation of life upon the earth. Can we assign to this a purpose?

The three answers that have been given to this question are spiritualism (in a broad sense), mechanism and agnosticism.

"Spiritualism" implies that life has come from the inorganic by an act of divine will. It does not necessarily imply, the author maintains, the doctrine of vitalism, but it usually implies that the universe is biocentric, adapted to production and perpetuation of life, and anthropocentric or adapted to the needs of man. "The details of the world are not made for man, but, if one believes in a spirit as Creator and Organizer of the universe, one may imagine the following sequence as willed by him: the Universe, Life, Conscience." Yet, quoting with approval the idea of Richet: "The expression *to will* is terribly human, but no one can refuse to recognize that gradual development of life and intelligence was included in the destiny of the terrestrial globe." The author thus seems to subscribe to the doctrine of predestination.

Materialistic mechanism on the other hand recognizes no organizing intelligence; its architecture is the result of a fortuitous concourse of atoms. Science discovers only a succession of events in the relation of cause and effect, involving neither volition nor direction; it is occupied with the "how" not the "why" of things, because there is no "why." The monist's universe is without beginning, purpose, or end, but perpetually in a state of evolution. Life is a property of inorganic matter, and under proper physical conditions has developed spontaneously from it either on this or on some other planet. There are in the living organism only physico-chemical properties, though of such complicated nature as to warrant the existence of distinct biological sciences. That some chemist some day may synthesize the living from the non-living is not beyond the bounds of expectation. The apparent purposefulness in organisms, which tends to perpetuate the life of the individual or of the species, is fortuitous unintentional, the result of the elimination, of the unfit, the ill-adapted. As Epicurus long ago held, the bird flies because it has wings, and one may not say that it has wings for the purpose of flight; man sees because he has eyes, the product of a slow evolution of which sight is the result. Man naively thinking of the universe in terms of human purpose is merely a transitory excrescence like mould upon the earth's crust, or passes like a flash into oblivion.

Agnosticism takes a middle ground between the two doctrines. For the agnostic the universe is the manifestation of a power which we cannot know and yet which we need to know in order to explain nature. Unable to escape the teleological impression which the universe gives him, the agnostic repudiates more or less clearly the idea of design. He "neither denies nor affirms the existence of a

Creator" and "carefully discards all that is metaphysical as unknowable and consequently uninteresting."

Science, occupied as it is solely with secondary causes, is unable to harmonize the conflicting views of those who think in terms of "spiritualism" or of materialistic mechanism. "Their convictions, both equally incapable of demonstration upon a scientific basis are a matter of personal feeling. For the one, the questions of beginning, of design, the 'why,' cannot be suppressed, and demand a reply which is found in the idea of God and in the immense synthesis of Universe, Life, and Man, the grandeur of which must be acknowledged; the second is not disturbed by metaphysical questionings, and the 'how' satisfies his curiosity."

Barring the unfortunate use of the confusing and inappropriate term "statistical" to which the reviewer has called attention, the book is throughout clear and exceedingly interesting. Adaptation is truly "*une effrayante question*." Successive generations of scholars viewing it each from a different angle have sought and found each their own answer. In the state of knowledge of the nineteenth century the formula of natural selection served well, but this stimulating book shows the inadequacy of this solution and states the problem as geneticists of the twentieth century see it. The present position may be weak and little more than a confession of ignorance. For in spite of all our knowledge of the morphology of chromatin, the touchstone of hereditary characters, we know nothing definite about the determination of form in growing organisms nor about any guidance of variation, but is not a confession of ignorance the sign of an inquiring spirit, and may it not mark progress toward a deeper knowledge of evolution and of adaptation?

EVOLUTION

THE WAYS OF LIFE.

By Richard Swann Lull. *Harper & Brothers*
\$3.00 $8\frac{1}{4} \times 5\frac{3}{4}$; xiii + 365 New York

This is an entertaining popular book on organic evolution with, quite fitly, a good deal of emphasis on the paleontological evidence. It can be highly recommended to the lay reader who wishes to inform himself about the concrete evidence regarding organic evolution.

LIVING ORGANISMS. *An Account of Their Origin and Evolution.*

By Edwin S. Goodrich.

Oxford University Press,
 $7\frac{3}{4} \times 5\frac{1}{4}$; 200 New York

An introduction to organic evolution by the Linacre Professor of Zoology and Comparative Anatomy in the University of Oxford. While containing little that is original, the book is an excellent brief review of the present status of knowledge regarding evolution, written with critical judgment and in an easy readable style. The evidence reviewed is mainly zoological.

THE EVOLUTION OF MAN. *Essays.*

By G. Elliott Smith.

Oxford University Press,
8 s. 6 d. $9 \times 5\frac{3}{4}$; vii + 157 New York

A republication of three essays originally prepared for delivery at popular lectures. The first has the title, "The Evolution of Man;" the second, "Primitive Man;" and the third, "The Human Brain." The common purpose of all three of these is to throw light on man's pedigree. While all students will not agree with the author's interpretations, his authoritative position in the field of anthropology and the skill and persua-

siveness with which he marshals his arguments, combine to make this a book which every serious student of the subject must read. The zoologist will be especially interested in the material on *Tarsius*.

THE ORIGIN AND EVOLUTION OF THE HUMAN DENTITION.

By William K. Gregory.

The Williams & Wilkins Co.
\$6.50 $6\frac{3}{4} \times 9\frac{1}{8}$; xviii + 548 Baltimore

This monograph is the standard reference work in the field. It assembles a great mass of evidence as to the fact and method of one phase of human evolution in a clear and convincing manner. A bibliography of 11 pages is appended.

PROMETHEUS OR BIOLOGY AND THE ADVANCEMENT OF MAN.

By H. S. Jennings. *E. P. Dutton & Co.*

\$1.00 $4\frac{1}{2} \times 6\frac{3}{4}$; vii + 86 New York

This latest addition to the well-known series of stimulating little books with Greek titles on general aspects of science. In this book the author ascribes greater importance to the environment in determining the nature of living things than most biologists do.

WHAT EVOLUTION IS.

By George Howard Parker.

Harvard University Press,
\$1.50 $4\frac{3}{4} \times 7\frac{1}{4}$; ix + 173 Cambridge

A book of the times, written to meet the demand created by the large and growing popular interest in evolution. The treatment is accurate, clear and concise. It makes its appeal on the clearness and cogency of the reasoning rather than upon illustrations.

THE EARTH BEFORE HISTORY.

Man's Origin and the Origin of Life.

By Edmond Perrier. Alfred A. Knopf

\$5.00 $6\frac{1}{2} \times 9\frac{1}{2}$; xxiv + 345 New York

This book, which is one of the volumes in the great series, "The History of Civilization," is, on the whole, the best available account within moderate compass of the evolution of life on the earth, up to man. It is not a popular work in the sense of being easy reading, but it more than compensates in its thoroughness and breadth for any possible lack of popular appeal. It will stand as an authoritative work of the first rank.

GENETICS

GENETICS AND EUGENICS. *A Text-book for Students of Biology and a Reference Book for Animal and Plant Breeders.*

By W. E. Castle Harvard University Press

 $9\frac{1}{4} \times 6\frac{1}{4}$; viii + 434 Cambridge,

A new edition of this well-known standard text in genetics. The material has been brought up-to-date. The viewpoint of the book is, of course, Mendelian in an absolutely orthodox sense. The treatment of the biometric side of genetics is not adequate.

MANUAL OF DAIRY CATTLE BREEDING.

By John W. Gowen.

The Williams & Wilkins Co.

\$3.00 $6 \times 9\frac{1}{4}$; 113 Baltimore

This is a laboratory manual to accompany the author's well-known treatise on *Milk Secretion*, published last year. From an intellectual viewpoint it represents a great advance in the laboratory teaching of animal husbandry in our agricultural colleges.

HEREDITY IN NERVOUS AND MENTAL DISEASES. *An Investigation by the Association for Research in Nervous and Mental diseases.*

By various authors. Paul B. Hoeber, Inc.

\$3.75 9×6 ; xxvii + 332 New York.

A series of papers by sixteen well-known contributors on various aspects of the inheritance factor in nervous and mental diseases, presented at the meeting of the Association for research in these subjects held in December, 1923. The volume contains little that is really new, but furnishes a useful summary of the present state of opinion in the field covered.

THE INHERITANCE OF MENTAL DISEASES.

By Abraham Myerson.

The Williams & Wilkins Co.

\$5.00 6×9 ; 336 Baltimore

This book, though badly written and badly edited in a style which constantly irritates the reader, nevertheless contains a mass of interesting, original observations on the hereditary factor in various abnormal mental conditions. A large number of detailed case histories are given. The work is one which cannot be neglected by any student of human genetics.

GENERAL BIOLOGY

THE SCIENCE OF BIOLOGY. *An Introductory Study.*

By George G. Scott.

Thomas Y. Crowell Co.

\$3.50 $8\frac{3}{4} \times 5\frac{3}{4}$; xii + 617 New York

This textbook is intended for elementary biology classes in colleges. It is unusually broad in its scope on both the animal and plant sides and appears to have been compiled with excellent judgment.

TEXT BOOK OF BIOLOGY. *For students in general, medical and technical courses.*

By William Martin Smallwood.

Lea and Febiger

\$3.75 $9\frac{1}{2} \times 6\frac{1}{4}$; xv + 393 Philadelphia

A new edition of an old and well established text book of general biology, which has proven its merit in earlier editions.

REGENERATION. *From a physico-chemical viewpoint.*

By Jacques Loeb.

McGraw-Hill Book Co. Inc.

\$2.00 $9\frac{1}{2} \times 6\frac{1}{4}$; ix + 143 New York

In this book, which, to the great loss of biology and the deep sorrow of his many friends, proved to be his last, Doctor Loeb brought together and rounded out his researches on regeneration in *Bryophyllum*. The essential result of the study was to show that equal masses of isolated sister leaves produced under equal conditions of illumination, temperature, etc., approximately equal masses of shoots and roots in equal time. On the basis of this mass relation Loeb attempted, with his customary ingenuity, to explain all the important phenomena of regeneration. Whether this theoretical interpretation is finally accepted or not, it will certainly prove enormously stimulating to research, as has so much of Loeb's other work.

ENZYME INTELLIGENCE AND WHENCE AND WHITHER.

By Nels Quenli. The Colwell Press, Inc.

6 x $8\frac{1}{2}$; 578 Minneapolis

This curious book is written by a registered pharmacist, who believes that enzymes are the ultimate indestructible and invisible units of life and are conscious and intelligent. He furthermore contends that enzymes produce and maintain

all living things we see, and that they come from what he calls "the invisible world of life," to which we return when we die. He has read the accessible book literature of biology very widely and has produced an entertaining volume, but it is much to be feared that Augustus DeMorgan would have classed him as a paradoxer.

EXPERIMENTELLE MORPHOLOGISCHE UNTERSUCHUNGEN. *Lipoid-, Glykogen- und Pigmentstoffwechsel (Handbuch der biologischen Arbeitsmethoden. Lieferung 171).*

By Ernst Leupold. Urban & Schwarzenberg M. 6,30. 7 x 10; 150 pp. Berlin

This number of the great Abderhalden hand book deals, in great detail, with the histological, physiological and biochemical technique essential to investigation in certain fields of experimental morphology.

THE ORGANIZATION OF LIFE. *A Revaluation of Evidence Relative to the Primary Factors in the Activity and Evolution of Living Organisms, Including a Factorial Analysis of Human Behavior and Experience.* By Seba Eldridge, with an introduction by H. S. Jennings. Thomas Y. Crowell Co.

\$4.50 $9\frac{1}{2} \times 6$; xv + 470 New York

A much too verbose, and consequently tiresome, theoretical discussion of all the major problems of biology, which seems, with singular pertinacity, to reach a conclusion on about all important topics, such as the inheritance of acquired characters, mechanism and vitalism, etc., which is diametrically opposed to that of most biologists who have thought about the matter. The general tone of Professor Jennings' introduction is very faintly laudatory. The book demonstrates that the author is an enormously industrious person.

IMMUNITY IN NATURAL INFECTIOUS DISEASE.

By F. d'Herelle (*Authorized English Edition by George H. Smith.*)

The Williams & Wilkins Co.

\$5.00 6 x 9; 399 *Baltimore*

In this book the author reviews the existing knowledge regarding the phenomenon of immunity to infectious diseases, from the point of view of his theory of the bacteriophage. The result is to make a highly interesting and valuable contribution to general biology. The subject is developed around the concept of the reactions of living things to stimuli. The book is divided into four parts, of which the first deals with the reactions of living matter in general; the second, with its reactions against inanimate agents; the third, with the reactions against bacteria; and the fourth with the ultraviruses and immunity against them. Though primarily written for the bacteriologist and medical man, the general biologist will find this book extremely interesting and stimulating.

HUMAN BIOLOGY

RICHTLINIEN FÜR KÖRPERMESSUNGEN. (*Und deren statistische Verarbeitung mit besonderer Berücksichtigung von Schülermessungen.*)

By Rudolf Martin. *J. F. Lehmanns Verlag*
2 Marks 9½ x 6½; 60 *München*

A very useful and sound treatise on the elementary technique of anthropometry. The material was drawn up particularly for the guidance of those working with school children, but it will be found valuable by a beginner in any field of anthropometry. The biometric methods outlined are only the simplest.

BIOLOGY AND HUMAN LIFE.

By Benjamin C. Gruenberg.

Ginn and Co.

\$1.72 8¾ x 5½; xiv + 592 + xi *Boston*

This high school textbook covers an enormous range; in fact, there is no department of biology which is not in some degree touched upon. Naturally, it nowhere goes to very great depths. The reference lists of reading, which follow each of the 51 chapters, are excellent.

TUBERCLE BACILLUS INFECTION AND TUBERCULOSIS IN MAN AND ANIMAL. *Processes of Infection and Resistance; a Biological and Experimental Study.*
By Albert Calmette.

The Williams & Wilkins Co.

\$8.00 6½ x 9; 714 *Baltimore*

To the general biologist this book is probably the best source from which to get a general comprehensive review of the present status of knowledge regarding the disease which, taking the world as a whole, kills more people than any other one in the normal, regular course of events. The viewpoint throughout this great monograph is primarily biological rather than narrowly medical. It is a book which should find a place on the shelves of every general biological library.

AN APPROACH TO SOCIAL MEDICINE.

By Francis Lee Dunham.

The Williams & Wilkins Co.

\$4.00 6 x 9; 242 *Baltimore*

A sane and somewhat philosophical guide to the social worker and especially to the worker in hospital social service. The student of any aspect of human biology will find it well worth reading.

APHORISMEN ZUM HEILPROBLEM.

*(Moderne Biologie Heft 9.)*By Prof. Dr. Hans Much. Curt Kabitzsch
Rm. 2 $7\frac{1}{2} \times 5$; 101 Leipzig

This is a highly theoretical discussion of the biological nature of disease, its course, and its treatment. A new therapeutic agent, "Omnadin," is discussed and temperature charts showing its action in fevers are given. From the rather vague statements given as to its composition omnadin seems comparable not to a shot-gun prescription, but to a whole flock of shot-guns.

DAS FRAUENPROBLEM IN IDEAL-STAAT. *Der Vergangenheit und der Zukunft.*By Margaret Weinberg. Curt Kabitzsch
 $7\frac{3}{4} \times 5$; vii + 85 Leipzig

An ultrafeministic tract of uplifting tendencies. The most interesting feature of the book is the historical treatment of feminism from the time of Plato down to date. There is a bibliography of three pages and a full index.

BIRTH CONTROL: FACTS AND RESPONSIBILITIES. *A Symposium Dealing with this Important Subject from a Number of Angles.*

Edited by Adolf Meyer. Chapters by Adolf Meyer, Margaret Sanger, Raymond Pearl, E. A. Ross, E. M. East, C. A. Rubenstein, Herbert A. Miller, R. McC. Chapman, R. A. Spaeth, C. C. Little, L. J. Cole, and Eleanor R. Wembridge.

The Williams & Wilkins Co.
\$3.00 $5\frac{1}{2} \times 7\frac{1}{2}$; xiv + 157 Baltimore

A treatise, of enormous respectability, on various aspects of birth control. It is made up of a number of separate and

quite unconnected essays by different persons, as indicated above. Probably the most significant essay in the volume is the last one, by Doctor Wembridge.

THE HAPPY CHILD.

By Dr. Henry L. K. Shaw (*Editorial Adviser*) and eight contributors

Dodd, Mead & Co., Inc.
\$1.00 $5\frac{1}{2} \times 7\frac{3}{4}$; lx + 126 New York

This is a book of excellent advice to young mothers, by eight persons of eminent standing in the social and medical fields. The period covered by the advice ranges roughly from birth up to school age.

THE CONQUEST OF DISEASE.

By David Masters.

Dodd, Mead & Co., Inc.
\$2.50 $5\frac{1}{2} \times 7\frac{3}{4}$; xv + 353 New York

This is a treatise, in popular language and style, on the outstanding points in the historical development of preventive medicine and public health. It is much better written than most books of its type, and can be recommended to the lay reader. Secondary school teachers of science will find it very useful.

DIE BIOLOGIE DES KRIEGES. *Die Ueberwindung des Krieges.*By G. F. Nicolai. Orell Füssli
Fr. 25 (Bd. I and II). Zurich

I. $6\frac{1}{2} \times 9$; xx + 324; II. $6\frac{1}{2} \times 9$; iv + 226

A new edition, with an introduction by Romain Rolland, of a well-known book which got the author into serious trouble when it was first published during the war. It is an interesting and stimulating book which no student of human biology

can afford to neglect, whatever may be his opinion as to the soundness of the conclusions reached.

ESSAYS IN PSYCHOPATHOLOGY.
Nervous and Mental Disease Monograph Series No. 43.

By William A. White.

\$2.50 $6\frac{1}{2} \times 9\frac{1}{4}$; x + 140 New York

A collection of essays and book reviews by a distinguished psychiatrist. The fundamental viewpoint of the book is that in the first place, man is not separate and distinct from his fellows or from the other components of his environment, but that he is only a place where for the time being certain forces are nucleated, and that as these forces grow out of the environment they resolve again into it; secondly, that so far as man is a container of energy he is not a closed but an open energy system, constantly deriving energy from the outside, constantly giving up energy to the outside; thirdly, that in considering man it may be useful to consider him in terms of energy rather than in terms of organs. These ideas can hardly be regarded as particularly original, but they are developed in an interesting way by the distinguished author.

GEBURTENRÜCKGANG UND RADFAHREN. *Ein Beitrag zum Problem des verschärften Geburtenrückgangs seit 1900.*

By J. Winkelbagen.

Selbstverlag des Verfassers

$5\frac{3}{4} \times 8\frac{3}{4}$; 50 Hamburg

The secret is out at last! Many people have puzzled their heads over the cause, or causes, of the world-wide decline in the birth rate in recent years. It is all due to riding bicycles, which also has sad effects upon the mental and physical characteristics of the offspring of those who indulge in this dreadful form of locomotion.

ZOOLOGY

ANATOMY AND PHYSIOLOGY OF THE HONEY BEE.

By R. E. Snodgrass.

McGraw-Hill Book Co., Inc.

$9\frac{1}{4} \times 6\frac{1}{4}$; xv + 327 New York

This book is a model of what a biological text ought to be. In a masterly way the author brings together and digests all that is known about the anatomy and the physiology of the honey bee, with the accurate, critical touch of one who knows the subject deeply and widely. It is a great pity that there are not available more treatises of this sort for the common forms of animal life.

FISHES OF THE GULF OF MAINE.

Bulletin of the U. S. Bureau of Fisheries, Vol. XL, Part I.

By Henry B. Bigelow and William W. Welsh.

Government Printing Office

\$2.00 $10\frac{3}{4} \times 7\frac{3}{4}$; 567 Washington

An excellent account of the taxonomy, with many ecological notes, of the fish fauna of the North Atlantic coastal region. A type of government publication much to be commended.

BRITISH BIRDS (Volume I).

By Archibald Thorburn.

Longmans, Green & Co.

\$5.50 6×9 ; xii + 176 New York

This is the first volume of a new edition, to be completed in four volumes, of Thorburn's well-known treatise on British birds. The feature of the work, of course, is the beautiful colored plates from the author's masterly paintings. Indeed, the plates may almost be said to constitute the work, for the text is trifling in amount. The original edition was expensive. The present is a popular edition greatly reduced in price. The reproduc-

tion of the plates on the smaller scale has, on the whole, been extremely well done. They make a strong appeal artistically as well as scientifically. This volume deals with the *Passeres* and contains 48 of the 192 colored plates which the whole work will include. It will be a useful addition to the library of any American bird lover.

JUNGLE DAYS.

By William Beebe. G. P. Putnam Sons
\$3.00 $6\frac{1}{2} \times 9$; v + 201 New York

This latest addition to the author's list of popular books on natural history will be found just as fascinating and thrilling as its predecessors. The observations with which it deals center about the jungle laboratory at Kartabo.

A LIST OF BRITISH APHIDES. *Including Notes on Their Synonymy, Their Recorded Distribution and Food Plants in Britain, and a Food-Plant Index.*

By J. Davidson.

Longmans, Green and Co.
\$4.50 $5\frac{3}{4} \times 8\frac{3}{4}$; xi + 176 London

This is a thorough piece of taxonomic work, giving check lists of the aphid species of Great Britain, together with their important synonyms, their food plants, and their distribution. There are also lists of the genera and important synonyms; of the food plants upon which the *Aphides* in the first section have been recorded in Britain, together with the species of *Aphides* found on them; and, finally, a bibliography of 18 pages.

INSECTS AND DISEASE OF MAN.

By Carroll Fox.

P. Blakiston's Son & Co.
\$4.00 $6\frac{1}{2} \times 9\frac{1}{2}$; xii + 349 Philadelphia

This is a systematic textbook of medical entomology for students of medicine and public health. The flavor of the book

throughout is taxonomic. It will furnish the student a sound grounding in this field.

BOTANY

BACTERIOLOGY. *A Text Book on Fundamentals.*

By Stanley Thomas.

McGraw-Hill Book Co., Inc.
\$2.50 $9\frac{1}{2} \times 6\frac{1}{2}$; xiii + 201 New York

This is an elementary general textbook on bacteriology for all kinds of undergraduate students, but it is especially directed towards the needs of the engineering student. It is a book which might well be recommended to the lay reader who wishes to gain, in short compass, a sound knowledge of the significance of modern bacteriology. It is clearly written and illustrated. Its greatest defect is that the references to the literature are meager in number and special in character, and, therefore, not well designed to guide the general reader in his progress to further and wider knowledge.

DICTIONARY OF BOTANICAL EQUIVALENTS. *German-English, Dutch-English, Italian-English.*

By Ernst Arscwager; French-English, by Edwina M. Smiley.

The Williams & Wilkins Co.
\$3.25 $7\frac{1}{2} \times 5$; 103 Baltimore

A handy little dictionary of technical botanical terms in the languages specified in the title, which now appears in a second edition.

GENERAL SYSTEMATIC BACTERIOLOGY. *History, Nomenclature, Groups of Bacteria.*

By R. E. Buchanan.

The Williams & Wilkins Co.
\$6.00 6×9 ; 400 Baltimore

This text-book is the first volume in a projected series of monographs in the

general field of systematic bacteriology. Of the three parts into which the book is divided, the first deals with the classification of the genera and higher groups of bacteria from an historical viewpoint, giving in detail the different schemes of classification which have been proposed in the period 1773 to 1922. The second part deals with biological codes of nomenclature and their application to the specific nomenclatorial problems of bacteriology. Finally, the bulk of the book is made up of an alphabetical list of the names which have been applied to groups of bacteria of higher rank than species—that is, genera and sub-genera—and their present nomenclatural status. The book closes with a bibliography covering 28 pages and indices covering 37 pages. A solid, substantial reference work.

BAKTERIOLYSE. *Einsichten und Aus-sichten (Mit besonderer Berücksichtigung der d'Herelle- und Much-Lyse). Moderne Biologie Heft 9.*

By Dr. Artur Haim. Curt Kabitzsch
Rm. 2 $7\frac{1}{2} \times 5$; 84 Leipzig

A concise account of the phenomenon of lysis in bacteria which discusses, without reaching any final conclusions, the probable biological nature of the processes involved. There is a bibliography of 13 titles.

PHOTOSYNTHESIS. *The Assimilation of Carbon by Green Plants.*

By Walter Stiles.

Longmans, Green & Co.
\$5.50 $5\frac{3}{4} \times 8\frac{3}{4}$; vii + 268 London

This is a technical work of first rank, assembling and reviewing critically the present state of knowledge regarding photosynthesis in plants. It will natur-

ally and necessarily find a place in every biological library which makes any claim to adequacy.

MORPHOLOGY

A TEXT BOOK OF VERTEBRATE EMBRYOLOGY. *Treated from the comparative standpoint.*

By Ruth L. Phillips. Lea and Febiger
\$3.50 $8 \times 5\frac{1}{2}$; xii + 302 Philadelphia

A brief elementary text book, well illustrated, and put together with a good deal of pedagogical skill. The first third of the book is devoted to the early development, and the last two-thirds to the embryology of the different organ systems. An excellent summary chapter of 38 pages at the end brings out the significance of the evidence from vertebrate embryology for organic evolution.

THE VERTEBRATE SKELETON FROM THE DEVELOPMENTAL STAND-POINT.

By J. S. Kingsley.

P. Blakiston's Son & Co.
\$6.00 $6\frac{1}{2} \times 9\frac{1}{2}$; viii + 337 Philadelphia

A ripe and authoritative treatise on comparative vertebrate osteology by a master in this field. There is a bibliography of 21 pages. Excellent indices close the work.

AN INTRODUCTION TO THE FINER ANATOMY OF THE CENTRAL NERVOUS SYSTEM BASED UPON THAT OF THE ALBINO RAT.

By E. Horne Craigie.

P. Blakiston's Son & Co.
\$3.00 $6 \times 8\frac{1}{4}$; 194 Philadelphia

A concise but adequate monograph on the anatomy of the central nervous system of that standard laboratory animal, the

albino rat. It is well illustrated with original drawings and carries a bibliography ten pages in length. Monographs of this type on standard laboratory animals are extremely valuable additions to the literature.

ÉTUDES SUR LES LÉMURIENS. *Anatomie comparée des fosses nasales et de leurs annexes.*

By Max Kollmann and Louis Papin.

Librairie Octave Doin

12 francs 6½ x 10; 61 Paris

The fascicle of the *Archives de Morphologie Générale et Expérimentale* is a technical piece of research on the morphology of the nasal fossae in the *Lemuridae*. The most important conclusions reached are: First, that the nasal anatomy indicates that the *Lemuridae* are to be divided into two distinct groups, the Madagascan forms and the extra-Madagascan forms; and, second, that the nasal fossae of *Lemuridae* are constructed on a type absolutely distinct from that of this region in the primates, with the exception of *Tarsius*, which shows the characteristic relations seen in the monkey. The results bring new evidence supporting the conclusion that *Tarsius* is an important form in any consideration of the evolution of the primates.

RECHERCHES ANATOMIQUES SUR L'APPAREIL GÉNITO-URINAIRE MALE DES SIRENIENS.

By G. Petit.

Librairie Octave Doin

40 francs 6½ x 10; iii + 326 Paris

An extensive piece of original research on the male genito-urinary organs of the Sirenians. It constitutes Fascicle 23 of the *Archives de Morphologie Générale et Expérimentale*. There is a bibliography covering six pages.

ALLGEMEINE VERGLEICHENDE FORMENLEHRE DER TIERE.

By Eduard Jacobshagen.

Dr. Werner Klinkhardt

Geh. Mk. 19.

Geb. Mk. 21. 50. 6½ x 10; viii + 258 Leipzig

An excellent treatise on a subject now much neglected in the biological discipline, general comparative morphology. The book is fully and well illustrated and contains a literature list of 202 titles. Translated into English it would make a first-rate textbook of comparative morphology for American colleges and universities.

PHYSIOLOGY

THE VITAL CAPACITY OF THE LUNGS.

By J. A. Myers.

The Williams & Wilkins Co.

\$3.25 6 x 9; 140 Baltimore

An interesting, if not very critical, expression of the great revival of interest among clinicians of the measurement of "vital capacity," by which is meant the number of cubic centimeters of air in a single expiration from the lungs. An excellent bibliography, covering 16 pages, is included.

HUMAN PHYSIOLOGY. *A Text-book for High Schools and Colleges.*

By Percy Goldthwait Stiles.

W. B. Saunders Co.

\$2.25 8 x 5½; 435 Philadelphia

The fourth edition of a popular elementary textbook. The book is reliable on technically physiological matters, but not always so on general biological points, as, for example, on page 408 where the statement regarding the hereditary influence of alcohol is directly opposite to the mature conclusions of all the recent critical experimental work in the field.

NUTRITIONAL PHYSIOLOGY.

By Percy Goldthwait Stiles.

W. B. Saunders Co.

\$2.25 8 x 5½; 307 Philadelphia

The fourth edition of a well-known elementary text on nutrition.

LE MÉTABOLISME DE BASE EN PHYSIOLOGIE ET EN PATHOLOGIE.

By Emile F. Terroine and Edgard Zunz.

Les Presses Universitaires de France

20 francs 6½ x 9½; 187 Paris

A very valuable summary of the present state of knowledge of basal metabolism, developed from the standpoint of physiology by the distinguished Professor of General Physiology in the University of Strasbourg, Doctor Terroine, and from the viewpoint of pathology by Doctor Zunz, the Professor of Therapeutics at Brussels. The book includes a bibliography of 21 pages in length, and is highly to be recommended as an authoritative treatment of the subject. It is published in an interesting new series entitled *Les Problemes Biologiques*, which is a collection of monographs appearing under the patronage of the Technical Committee for Natural Sciences of the *Presses Universitaires de France*.

FOOD AND HEALTH.

By R. H. A. Plimmer and Violet G. Plimmer.

Longmans, Green & Co.

\$1.25 5 x 7½; 64 London

This is a concise treatise, in popular language and style, setting forth for the lay reader the present state of knowledge regarding the physiology of nutrition. It is well written and illustrated and will form a valuable addition to secondary school and college biological libraries.

HEALTH AND ENVIRONMENT.

By Leonard Hill and Argyll Campbell.

Longmans, Green and Co.

\$4.20 8¾ x 5¾; xi + 208 New York

In this book is embodied, in rewritten and reëdited form, the substance of three memoirs originally issued as reports of the Medical Research Council, having the titles: "The Science of Ventilation and Open Air Treatment, Parts I and II," and "The Kata-Thermometer in Studies of Body Heat and Efficiency." These reports were of great interest and value to physiologists and it is advantageous to have the material now available in book form for wider circulation. The student of ecology will find this work extremely suggestive.

BIOCHEMISTRY

THE FATS.

By J. B. Learthes and H. S. Raper.

Longmans, Green and Co.

\$4.50 8¾ x 5¾; xi + 208 New York

A new edition of what is by common consent regarded as the authoritative treatise on the biochemistry of the fats. Considerable new material has been added and the extensive bibliography brought up to date.

FUNDAMENTALS OF BIOCHEMISTRY. In Relation to Human Physiology.

By T. R. Parsons.

The Williams & Wilkins Co.

\$3.00 4¾ x 7½; xii + 295 Baltimore

The second edition of what is one of the best of elementary treatises on biochemistry for the student of general biology. The principal changes from the first edition consist in the addition of a discussion of insulin, and a discussion of Werner's views regarding the constitution of urea. Brief, but well chosen, bibliographies follow each chapter.

PRACTICAL PHYSIOLOGICAL CHEMISTRY.

By Sydney M. Cole.

The Williams & Wilkins Co.

\$4.00 9 x 5½; xvi + 405 Baltimore

The sixth edition of a well-known laboratory manual.

THE EFFECTS OF IONS IN COLLOIDAL SYSTEMS.

By Dr. Leonor Michaelis.

The Williams & Wilkins Co.

\$2.50 5 x 7½; 108 Baltimore

Contains the substance of lectures given in April and May 1924 by Professor Michaelis at various American universities on the following topics: Adsorption; electric phenomena produced by the adsorption of ions; the origin of the electric double layers; the properties of charcoal; the connection between discharge, adsorption and flocculation; the so-called Donnan equilibrium; lyotropic effects of ions; mixtures of electrolytes. The book lacks an index, which seems a pity, and there are no specific, documented, bibliographical references.

PHYSICAL CHEMISTRY. *Its Bearing on Biology and Medicine.*

By J. C. Philip.

Longmans, Green and Co.

\$2.80 7½ x 5½; viii + 367 New York

In this third edition of a well known elementary text the chief addition has been a discussion of hydrogen ion concentration and buffer mixtures in the last chapter. Throughout the book the material has been brought up to date, with the addition of bibliographical references to recent works. This is one of the best of the numerous books dealing with physical chemistry from the viewpoint of the needs of the biologist.

CHEMICAL DYNAMICS OF LIFE PHAENOMENA.

By Otto Meyerhof.

J. B. Lippincott Co.

8½ x 5½; 110 Philadelphia

This book is made up of a series of lectures given in the spring of 1923 at various American universities. The topics dealt with are: The physico-chemical mechanism of cell respiration; autoxidations in the cell; chemical relations between respiration and fermentation; the transformation of energy in muscle; the energetics of cell processes. A bibliography of 163 titles is appended.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. Lieferung 166.

Fermentforschung. Containing following articles: *Labfermente*, by S. G. Hedin; *Reindarstellung des Pepsins*, by C. A. Pekelharing; *Arginase und Urease*, by Theodor Sabalitschka; *Alkoholoxydase der Essigbakterien*, by Jakob Meisenheimer; *Darstellung und Nachweis von Oxydasen und Katalasen pflanzlicher und tierischer Herkunft.* *Methoden ihrer Anwendung*, by Robert Chodat; *Indikatormethoden zum Nachweis von Zelloxydationen*, by Werner Lipschitz; *Reindarstellung der Katalasen*, by H. v. Euler; *Carbohydrasen-Proteasen und Peptasen*, by Julius Wohlgemuth.

Urban & Schwarzenberg

M. 10.50 7 x 10; 260 Berlin

The scope of this number of Abderhalden's handbook is sufficiently indicated by the subtitles for the different parts.

THE NATURE OF ENZYME ACTION.

By Sir W. M. Bayliss.

Longmans, Green and Co.

\$3.25 6½ x 9½; i-viii, 200 London

This is the fifth edition of this book, which is published in the series of "Mono-

graphs on Biochemistry." The chief additions and corrections in this edition relate to the methods of purification of enzymes and to the problem of equilibrium in heterogeneous catalysis. The book was put through the press during the lamented author's last illness. There is a bibliography of nearly 20 pages in length.

LA CONCENTRATION EN IONS HYDROGÈNE ET SA MESURE PAR LA MÉTHODE ELECTROMÉTRIQUE. *Application aux variations de l'équilibre acide-base du sang, à l'état physiologique et à l'état pathologique—action de colloïdes électriques en injection intraveineuse.*
By Maurice Vincent.

Librairie Scientifique J. Hermann
50 cents. $6\frac{1}{2} \times 10$; 102 Paris

A useful, concise treatise on the significance of hydrogen ion concentration in various biological matters, but with special reference to the acid-base equilibrium of the blood. There is a bibliography covering 13 pages.

PHYSIOLOGICAL AND CLINICAL CHEMISTRY.

By Wm. A. Pearson and Joseph S. Hephurn.
Lea and Febiger

\$4.00 $5\frac{1}{2} \times 8$; xvi + 306 Philadelphia

A new textbook of physiological chemistry for students of medicine. It is interleaved for notes and is intended to be used both for study and reference and as a laboratory guide. It works out in the end, however, to be essentially an excellent laboratory outline.

BIOMETRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. Lieferung 165. *Wahrscheinlichkeitsrechnung, Methoden der kleinsten Quadrate, Kollektivmasslehre.*

By G. Polya, and *Biometrik und Variationsstatistik*, by Paul Riebesell.

Urban & Schwarzenberg,
M. 6.60 7×10 ; 162 Berlin

This number of Abderhalden's Handbook of Biological Technique deals in an elementary but, on the whole, sound way with the theory of probability and biometric technique. For American readers it possesses no advantage over other readily available textbooks in these subjects, but will probably serve a useful purpose in Germany.

AN INTRODUCTION TO THE METHODS OF ECONOMIC STATISTICS.

By William Leonard Crum and Alson Currie Patton.
A. W. Shaw Co.

\$6.00 $5\frac{3}{4} \times 8\frac{1}{2}$; xii + 493 Chicago

Another textbook of statistical methods, in this case with special reference to economic data. It covers about the same ground as other well known textbooks in the field, with rather more attention to the type of correlation which arises in connection with time series than is usually given.

SEX

THE INTERNAL SECRETIONS OF THE SEX GLANDS. *The Problem of the Puberty Gland.*

By Alexander Lipschutz.

The Williams & Wilkins Co.
\$6.00 $5\frac{3}{4} \times 8\frac{1}{2}$; xviii + 507 Baltimore

A general treatise on the endocrine physiology of the sex glands, based primarily on the author's personal researches, but reviewing generally from that point of view the literature in the field. The work is extensively illustrated, and furnishes long bibliographies of the original literature, following each chapter. The sub-

jects treated are: Sexual dimorphism and the secondary sexual characters; the results of castration; the internal secretions of the sexual glands; the seat of production of the internal secretion of the testicle; the seat of production of the internal secretion of the ovary; the sex specific action of the testicular and ovarian hormones; the question as to the isolation of the sexual hormones; the seminal vesicles and the prostate gland; intersexuality; eunuchoidism; sexual hormones and morphogenesis; the problem of rejuvenation. The distinguished authority, Prof. F. H. A. Marshall, says in his introduction that "as a guide to the literature of a branch of endocrinology that has grown rapidly in recent years the work should be of great value." It is well indexed.

AN INTRODUCTION TO SEXUAL PHYSIOLOGY.

By F. H. A. Marshall.

Longmans, Green & Co.

\$2.75 $5\frac{3}{4} \times 8\frac{3}{4}$; xii + 167 London

This book is intended to meet the needs of biological, medical and agricultural students for a more concise treatment of the subject of sexual physiology than that of the author's well-known book, "The Physiology of Reproduction." It is completely authoritative and admirably suited to fulfil this real need.

SEX AT CHOICE.

By Mrs. Monteiish Erskine.

G. P. Putnam's Sons

\$2.50 $5\frac{1}{2} \times 7\frac{1}{2}$; xxvi + 187 New York

This entertaining volume, written in a spirit of deep earnestness and high moral fervor, with a preface by the author's husband, who is a Member of Parliament, sets forth what the author firmly believes

to be the true secret of controlling the sex of offspring at will. The theory has but one slight defect; it is not true. The thoughtful reader will find in it an interesting example of the well-known fact that meticulous honesty and sincerity are not the only requirements for a sound and successful scientific methodology.

PUBERTÉ ET MATURITÉ SEXUELLE. (*Étude histologique et expérimentale.*)

By Ed. Retterer. *Librairie Octave Doin*

10 francs $5\frac{3}{4} \times 9$; x + 208 Paris

This is a record published in book form of a series of investigations by the author on the significance of the interstitial cells of the testis and ovary. The general conclusion reached is that these cells play a very slight, if any, rôle in the endocrine activity of these organs.

REJUVENATION BY GRAFTING.

By Serge Voronoff.

Adelphi Co.

\$6.00 $5\frac{3}{4} \times 8\frac{3}{4}$; 224 New York

This is an English translation of Voronoff's much discussed book, "Quarante-trois greffes du singe à l'homme." The evidence offered falls a long way short of demonstrating that the grafting of anthropoid testicular tissue into men produced any real rejuvenation, or retardation of senescence.

ÜBER DEN INZEST.

By Heinrich Többen.

Franz Deuticke

3 Marks $10\frac{1}{2} \times 7$; vi + 92 Leipzig

A gruesome record of the case histories of persons convicted of incestuous practices. It has the value of an original document for students of dysgenic and anti-social phenomena.

PSYCHOLOGY AND BEHAVIOR

CHIMPANZEE INTELLIGENCE AND ITS VOCAL EXPRESSIONS.

By R. M. Yerkes and Blanche W. Learned.

The Williams & Wilkins Co.\$3.50 5 x 7½; 157 *Baltimore*

The senior author reviews in the first part of this book rather briefly some of the more outstanding results of his study of the mental traits of a pair of chimpanzees. The second part of the book gives in detail the reduction to musical notation of the various sounds emitted by these chimpanzees in the course of their daily life. A bibliography of 12 titles closes the book, which would have been improved by the addition of an index.

SOCIAL PSYCHOLOGY.

By Knight Dunlap.

The Williams & Wilkins Co.\$4.00 6 x 9; 261 *Baltimore*

A well written treatise by a psychologist of the first rank on the psychological factors or elements in social organizations of various sorts. The topics discussed are: The field of social psychology; sex differences; marriage and the family; religious organization; civic and martial organization; the condition of social progress; the principles of social organizations; and propaganda. The book can be recommended as highly entertaining as well as soundly informative.

ZUM GEGENWÄRTIGEN STAND DER LEHRE VON DEN REFLEXEN.

By Dr. M. Minkowski. *Orell Füssli*Fr. 4.50 6½ x 9½ (paper); 61 *Zürich*

This book constitutes the first number of a series of *Neurologische und psychiatrische Abhandlungen* under the general editorship of Professor von Monakow. It is a thorough-going review, with extensive bibliographical documentation, of the present state of knowledge regarding reflexes. A considerable section of the work deals with the interesting subject of the embryonic development of reflex activity.

ALMOST HUMAN.

By Robert M. Yerkes.

The Century Co.\$3.00 5½ x 8½; xxi + 278 *New York*

This book deals in the main with an account of the well-known colony of anthropoids established and maintained by Señora Rosalia Abreu on her estate near Havana. At the same time it contributes a great deal, out of the author's wide fund of knowledge, to our understanding of the psychology of the primates below man. There is a bibliography of 20 titles, but no index.

ANIMALS LOOKING INTO THE FUTURE.

By William A. Kepner.

*The Macmillan Co.*5½ x 8; ix + 197 *New York*

This a valuable and important little book. It should be in every biological library. It presents in a thoroughly sound and, at the same time, entertaining manner, the established facts regarding the teleological element in the behavior of lower organisms.



SKELTON OF EOhippus IN AMERICAN MUSEUM OF NATURAL HISTORY, FOUND IN LOWER EOCENE OF BIGHORN BASIN, WYOMING, IN 1911

THE QUARTERLY REVIEW *of* BIOLOGY



THE EVOLUTION OF THE HORSE. A RECORD AND ITS INTERPRETATION

By W. D. MATTHEW

The American Museum of Natural History

INTRODUCTION

THE geological record of the Ancestry of the Horse is one of the classic examples of evolution. For this there are several reasons. First, the horse is a familiar animal; everyone knows what it is like, its habits, and is interested in learning how it got that way. Second, its fossil record is the most complete among the larger animals, and third, the outstanding changes in teeth and skeleton are obvious and easy to specify, and it is not difficult to understand their significance in animal mechanics and adaptation.

It has been a classic for fifty years or more, but the fossil evidence has vastly increased during that time, and especially during the last twenty or thirty years. Where Marsh and Cope and Leidy depended upon a few specimens, mostly fragmentary, we have today great series of complete skulls and skeletons; where their knowledge of the geologic succession was sketchy and generalized, ours is far more exact and certain. Yet there is very little to alter in what they had to

say, although much to add, and it is the highest tribute to the insight and sound scientific method of these pioneers that their early work remains with but little change as the foundation of our present knowledge.

In this essay I shall attempt to give an outline first of the facts of record, the fossil evidence as it stands today, and second of the interpretation of that record, what it signifies and what it proves in the light of various aspects of modern research. So far as the facts are concerned, they are not cited from authority, but with very few exceptions are stated from first-hand knowledge and observation. Much of the detailed evidence on which these statements rest has been published by various authors, and the more important publications are listed at the end of the paper. Much of it is still unpublished material in the American Museum and elsewhere collected principally during the last few years. This unpublished material is responsible for various minor discrepancies between statements here made and those of previous writers. The interpretation of the evidence represents my

EVOLUTION OF THE HORSE

The Ancestry of the Horse has been traced back through a long series of successive stages, represented by fossil skeletons found in the successive formations of the Age of Mammals, to small quadrupeds with four toes on the fore foot, three on the hind foot, with low-crowned simple teeth, small brains, and various other features common to all possible mammals.

The earliest known form is a small quadruped, *Hyracodon*, which lived about 50 million years ago. It was a small animal, about the size of a dog, with a long neck and a small head. It had four toes on the fore foot and three on the hind foot. Its teeth were simple and low-crowned. Its brain was small. It was a typical mammal of its time.

- A. Hyracodon, the earliest form of the horse.
- B. *Protorosaurus*, of the Eocene.
- C. *Leptacodon*, of the Eocene.
- D. *Archaeotherium*, of the Eocene.
- E. *Palaeotherium*, of the Eocene.
- F. *Palaeotherium*, of the Eocene.
- G. *Palaeotherium*, of the Eocene.
- H. *Palaeotherium*, of the Eocene.
- I. *Palaeotherium*, of the Eocene.
- J. *Palaeotherium*, of the Eocene.
- K. *Palaeotherium*, of the Eocene.
- L. *Palaeotherium*, of the Eocene.
- M. *Palaeotherium*, of the Eocene.
- N. *Palaeotherium*, of the Eocene.
- O. *Palaeotherium*, of the Eocene.
- P. *Palaeotherium*, of the Eocene.
- Q. *Palaeotherium*, of the Eocene.
- R. *Palaeotherium*, of the Eocene.
- S. *Palaeotherium*, of the Eocene.
- T. *Palaeotherium*, of the Eocene.
- U. *Palaeotherium*, of the Eocene.
- V. *Palaeotherium*, of the Eocene.
- W. *Palaeotherium*, of the Eocene.
- X. *Palaeotherium*, of the Eocene.
- Y. *Palaeotherium*, of the Eocene.
- Z. *Palaeotherium*, of the Eocene.



PLEISTOCENE HORSE SKULL
This skull is from a horse that lived about 10,000 years ago. It is a typical horse skull of its time, with a large brain and a long neck.

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PLEISTOCENE EPOCH

PLEISTOCENE EPOCH

MIOCENE EPOCH

OLIGOCENE EPOCH

EOCENE EPOCH

own views, coincident in the main with those of most students of fossil vertebrates, but with various shades of divergence

which more positive confrères may challenge as "errors" if they will. Within the space allotted it would be impossible

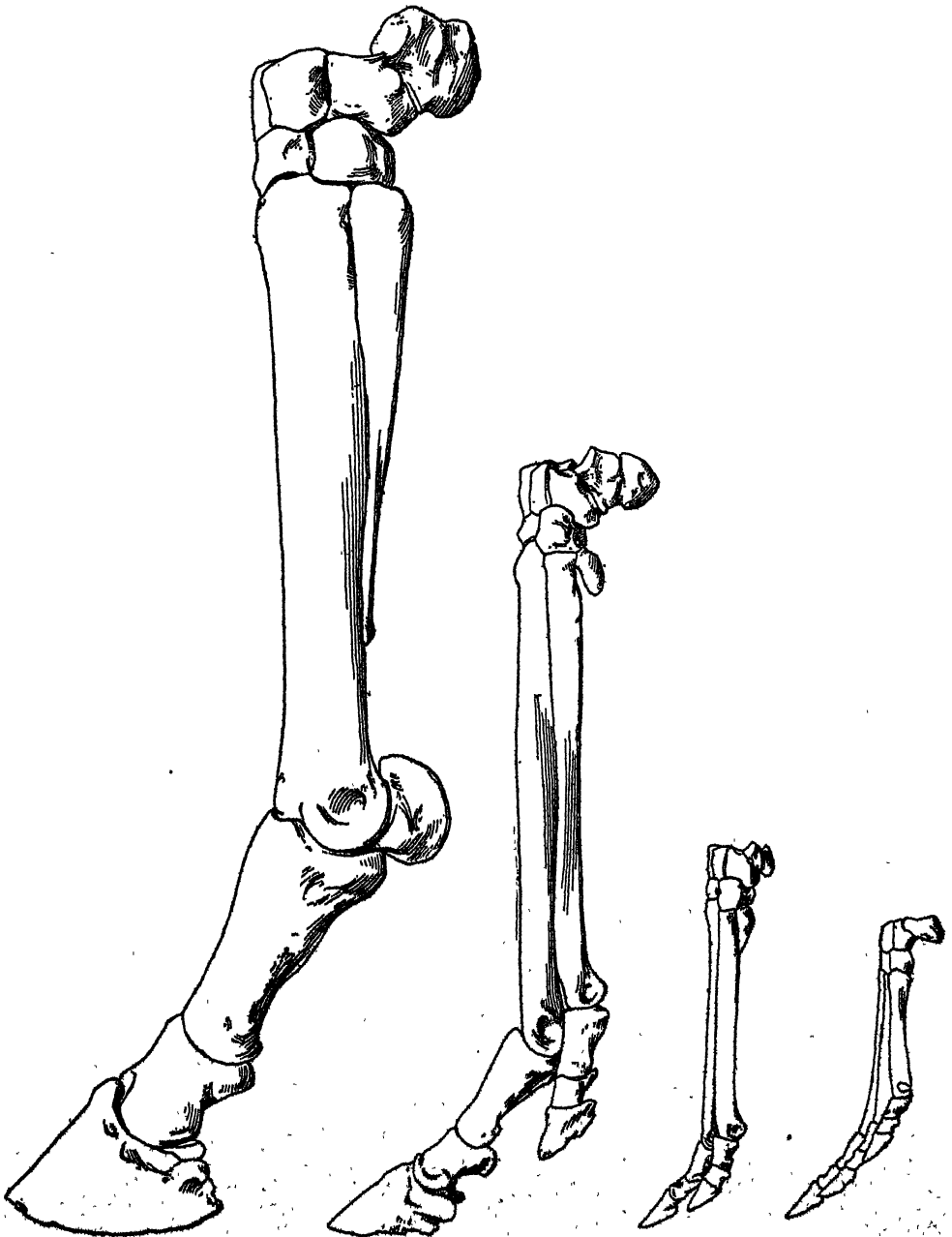


FIG. 2. STAGES IN THE EVOLUTION OF THE FORE FOOT: EOHIPPUS, MESOHIPPUS, MERYCHIPPUS AND EQUUS. External view, showing the progressive disappearance of the fifth and reduction of the fourth digit.

to discuss such divergences of interpretation as may appear by comparison with the authorities cited. The views here outlined appear to me reasonable, consistent with each other, and conformant with what I know of nature and of natural science.

The illustrations are mostly from the files of the Department of Vertebrate Palaeontology. I have added a few diagrams and altered others to bring them up to date.

CHARACTERS OF THE SKELETON

The documents which constitute our record of the Ancestry of the Horse are skeletons or various parts of skeletons. The soft parts are never preserved as fossils. In order to understand what the fossils signify we must first know what the skeleton, bones and teeth of a horse are like, and how they differ from those of other animals.

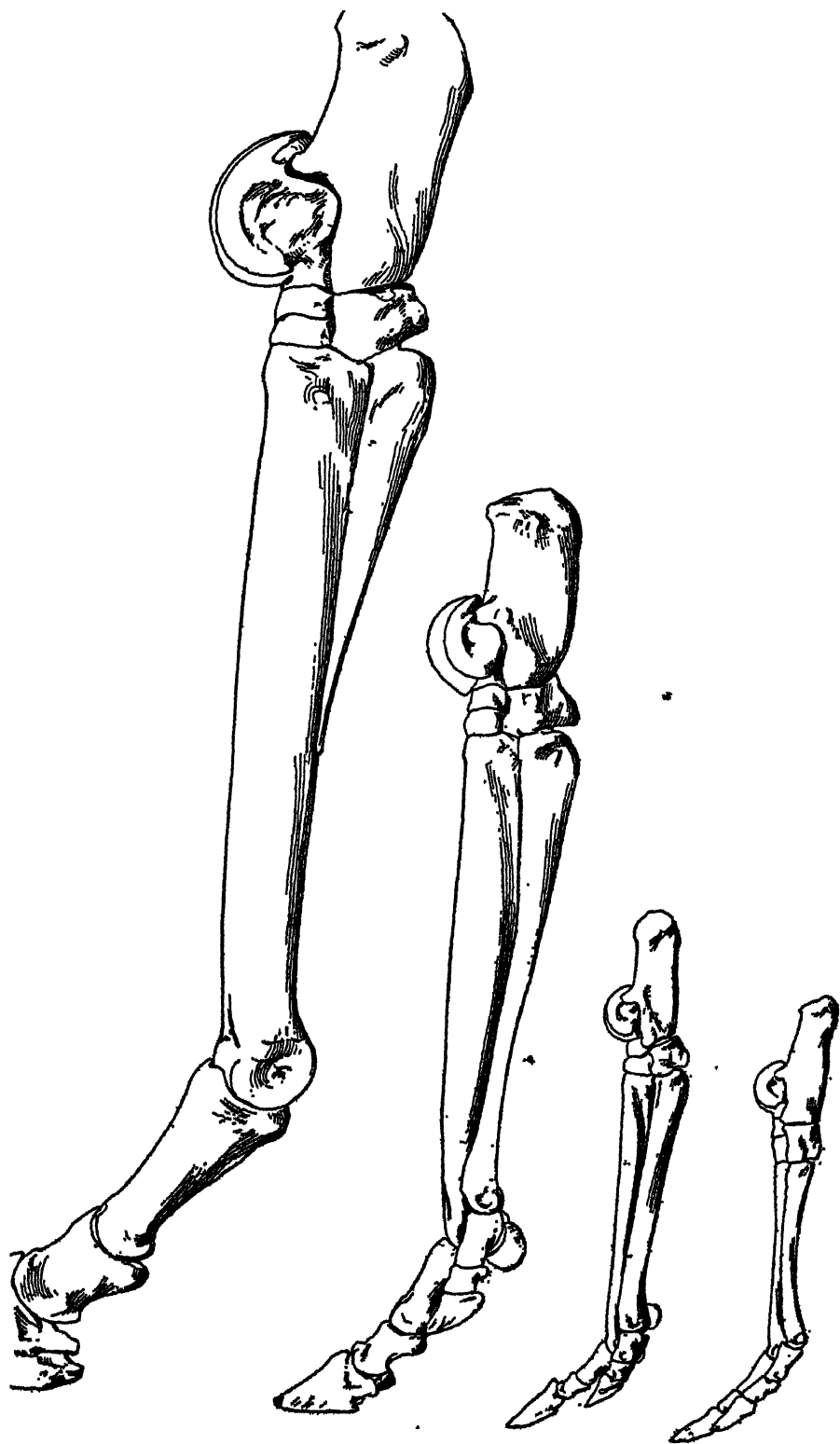
Compared with the skeleton of man, there are many contrasts in proportion, and yet the underlying construction has much in common. The skull of a man is short and round and almost all brain-case; the skull of a horse is long and almost all face; yet they are made up of the same bony elements sutured together and related to each other in the same way, the processes for attachment of muscles, foramina for nerves and blood-vessels, relations of the teeth and location of various sense organs all correspond. The contrast is due to differences of proportion, of size and form of different bones or parts of bones; the fundamental construction is identical.

The face of the horse is extended far forward to accommodate a powerful battery of grinding teeth and a set of cropping teeth in front of them. These teeth are forty-four in number, three incisors, a canine, four premolars and three molars on each side of upper and of lower jaw; and

all the permanent teeth except the molars and anterior lower premolars (p_1) are preceded by milk teeth. The p_1 however is very small and early lost, and the upper canines are developed only in the male. There are thus ordinarily only forty; fourteen cropping and twenty-six grinding teeth. In man the teeth are reduced to thirty-two—two incisors, a canine, two premolars and three molars on each side above and below.

The cropping teeth are somewhat like our incisors but longer crowned, with an inner crest separated by a deep pocket from the outer crest. This pocket is known as the "mark" because with the wear of the tooth it is gradually reduced and finally obliterated, and one can judge of the age of a horse by the size of the "mark."

The grinding teeth (excepting the first upper premolar which is small and simple) are square prisms with a complex pattern of infolded enamel on the wearing surface, and the valleys between the enamel filled with "cement," which also invests the outer surface. The prism is pushed up in the jaw as it wears off on the surface, and the harder enamel forms at all stages of wear little ridges supported by dentine on one side (originally the *inside* of the tooth) and cement on the other. The cement is deposited on the tooth as it comes up in the jaw, before it breaks through the gums, but the enamel and dentine are formed at an earlier stage in the development of the tooth, while it is within the dental chamber. These prism-shaped teeth are composed of the same parts as human teeth, but the crown is greatly elongated vertically (hypsodont) and the cement is a new structure deposited by special glands which are elaborated from the lime-secreting alkaline salivary glands. The crowns of the teeth push up through the gums and begin to wear before the roots are completed, but at 5-8 years the roots close, and thenceforth



the tooth ceases to grow at the base, and is pushed up and worn down until it is used up, when the animal dies because it can no longer chew its food.

The record shows the evolution of these

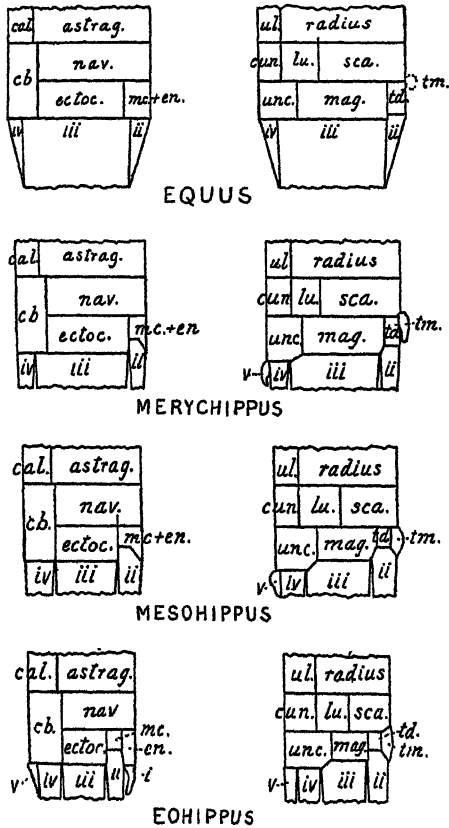


FIG. 4. DISPLACEMENT OF THE CARPAL AND TARSAI BONES IN EOhippus, MESOhippus, MERYCHIPPUS AND EQUUS

The median carpals and tarsals are broadened out with the growth of the third digit, the lateral metapodials are progressively pushed out from the support of the foot, while the lateral podial bones, except the trapezium, acquire a footing on the head of the third metapodial, thereby strengthening the carpal and tarsal joints at some expense in flexibility.

long-crowned complex grinders from small short-crowned simple teeth much more like the human molar.

The skeleton of a horse likewise corresponds in construction to that of a man, again with wide differences in proportions.

There are seven neck vertebræ, but very much longer than in man, although the parts and processes correspond. There are nineteen rib-bearing vertebræ as against twelve in man, and they carry quite high median spines making the crest of the shoulders. The ribs and breastbone form a box which is deep and narrow in contrast to the wide shallow chest of man. The pelvis has the same parts and relations, but wholly different proportions from the basin-shaped pelvis of man. The tail is long and free instead of the curled-in vestige retained in man. The shoulder-blade is long instead of broad. The limb bones are strong and heavy instead of long and slender.

In man, as in all primitive and many modern mammals, the fore arm and leg have two separate bones, radius and ulna, tibia and fibula, which can move one around the other so as to permit rotation of the hand or foot. This is wholly lost in the horse. Radius and ulna are solidly co-ossified, and the shaft of the ulna is a slender thread plastered against the back of the radius. The fibula is similarly reduced and co-ossified, except that part of the shaft has disappeared instead of consolidating with the tibial shaft.

The feet are still more specialized in the horse. It walks, so to speak, upon its middle fingernail, and the side toes have disappeared. The one remaining digit is nearly as long as the other segments of the limb, the metapodials or cannon-bones being much elongate with cylindrical shafts. Behind these shafts are the splint bones, vestiges of the second and fourth digits, and occasionally in modern horses a tiny nodule of bone may be found by careful dissection, which is the last trace of the fifth digit of the fore foot. The form of the bones and joints differs from that in man in numerous details which adapt the limbs and feet for locomotion,

giving strength and powerful leverage at the expense of most of its flexibility.

The record shows the progressive stages

the majority of existing mammals, which, like man, had five toes on each foot, and the limb and foot much better adapted

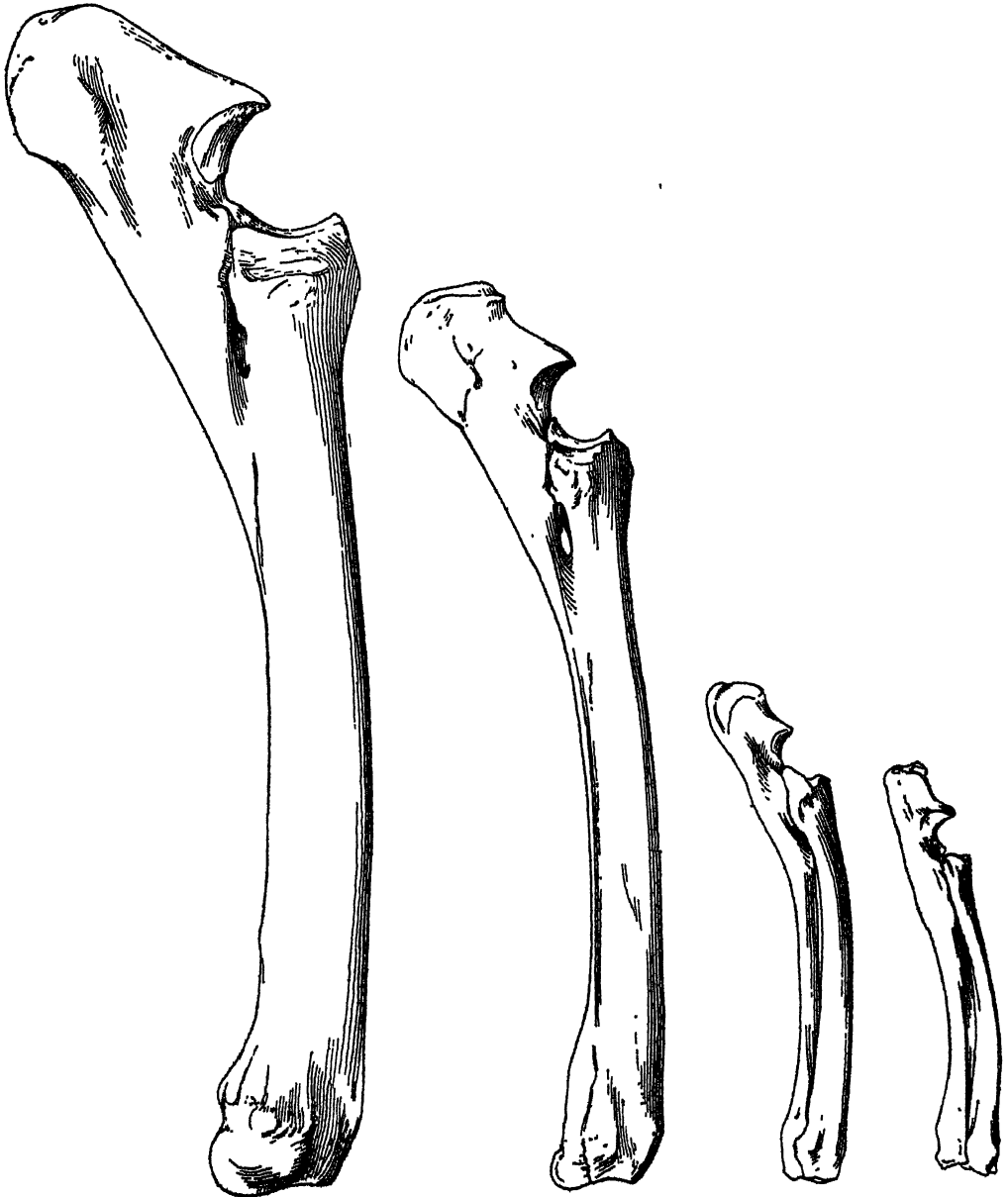


FIG. 5. PROGRESSIVE CONSOLIDATION OF RADIUS AND ULNA: EOHIPPIUS, MESOHIPPIUS, MERYCHIPPUS AND EQUUS

in the evolution of this highly specialized organ of locomotion from a foot much nearer that of primitive mammals and of

to various uses. The earliest known stage in the ancestry of the horse has four complete separate digits of nearly equal

size on the fore foot, and three on the hind foot, with vestiges of the two missing ones. Future discovery may enable

various textbooks, especially Chubb (1921), Lydekker (1912), and Sisson (1910).

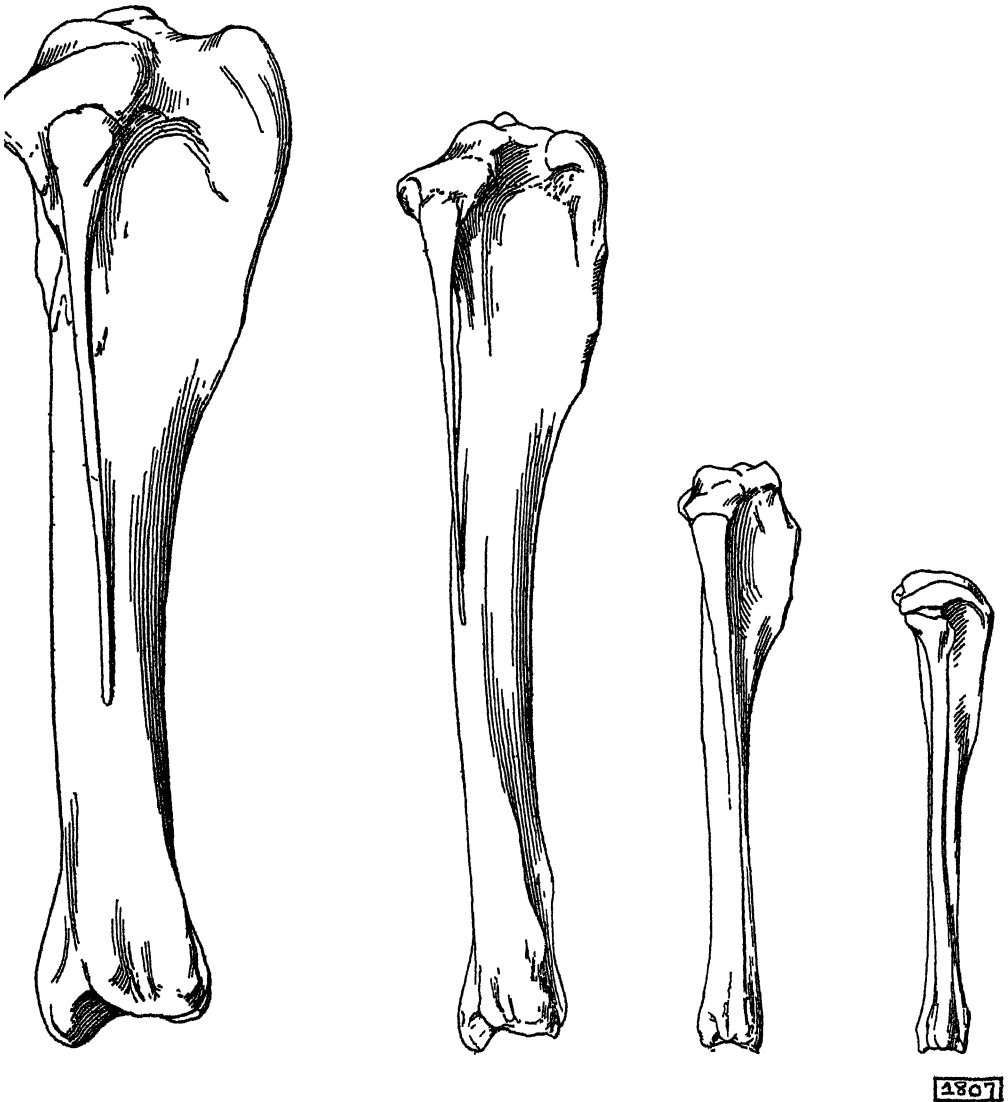


FIG. 6. PROGRESSIVE REDUCTION OF THE FIBULA: EOHIPPUS, MESOHIPPUS, MERYCHIPPUS AND EQUUS

us to trace the ancestry back to a five-toed form.

Excellent accounts of the osteology of the horse, the development of the teeth, and its general anatomy may be found in

LIVING SPECIES OF HORSES AND THEIR RELATIVES

The breeds of the domestic horse vary widely in size and considerably in general

proportions, as well as in color and various superficial characters. The extremes of size in the Shetland pony and the Percheron draft-horse, of proportions in the slim compact race-horse and the massive plow-horse, are wide apart. Yet, aside from the characters on which the emphasis of breeding has been placed, all domestic horses agree very closely. The pattern of the teeth agrees closely throughout; so also there are innumerable details throughout the skeleton which are constant or very slightly varying. And all interbreed freely with no loss of fertility in the offspring.

The domestic ass has no great diversity of breeds, and is distinguished from the horse by a number of constant characters in the teeth, skull and skeleton, as well as by the sterility of the hybrid offspring. In the tooth pattern there are some details that are not very obvious but quite constant—notably the absence of the "cabal-line fold" of the upper molars.

* The various wild species are in varying degree infertile with the domestic horse and with each other, and distinguished by surface characters often obvious enough, but all are much alike in teeth and skeleton and not easily distinguished. The wild ass of North Africa is believed to be the progenitor of the domestic species, and among the true wild horses and feral races found in Central Asia are probably the descendants of the original wild stock of the domestic horse. In Africa south of the Sahara are several kinds of zebras usually grouped in three distinct species still living; a fourth, the quagga, became extinct during the nineteenth century. The zebras are readily distinguished by the color pattern, and there are some differences among them in the form of the skull and other details, but in the teeth they are almost indis-

tinguishable from each other or from the domestic horse.

All the species of the horse family are thus very much alike in teeth and skeleton, and by this criterion nearly related to each other. They stand in a group apart, widely different from any other animals, so much so that they were formerly placed by naturalists in a distinct order Solipeda. The great anatomist, Richard Owen, recognized however that underneath the diversity of form and proportions there were certain underlying identities in construction of skeleton, pattern of teeth, and other anatomical characters, between horses, tapirs and rhinoceroses, and united them in the order Perissodactyla or odd-toed ungulates, separating them from the Artiodactyla or even-toed ungulates including most other hoofed animals (pigs and peccaries, hippopotami, camels, deer, giraffes, antelopes, sheep and cattle).

The astragalus in Perissodactyla has always an oblique pulley-joint with the tibia, and a nearly flat distal facer; the axis of symmetry in the hind foot passes always through the center of the middle digit; the premolars always are more or less like the molar teeth, and later researches than Owen's have shown that there is always the same fundamental pattern in the molar teeth of Perissodactyla although variously modified in the different families.

The rhinoceroses have three toes on each foot, short, stout, somewhat spreading, and of subequal size, and the teeth moderately high-crowned with a comparatively simple pattern of an outer crest and two oblique cross crests, and little or no cement. Their front teeth have either been wholly lost or a single pair of stout lower tusks remains, sometimes also a pair of upper tusks. All

modern rhinoceroses have horns, one, or two arranged tandem.

The tapirs have four toes on the front foot, and three on the hind foot, their cheek teeth are short-crowned, with a simple pattern of cross crests, united by an external loop in the upper teeth; the front teeth are of cropping type, somewhat as in the horse, but lacking the inner crest and "mark." The muzzle is developed into a prehensile proboscis or short trunk, and the conformation of the skull considerably modified for attachment of the necessary muscles.

These three types of hoofed animals are very diverse in their external appearance, habits of life, and environment. The horses, living wholly in the open plains and feeding upon short dry grasses, swift footed, unarmed, escaping their enemies by flight, represent one perfected special adaptation. The rhinoceroses, living mainly in the bush and open forests, feeding upon the coarser grasses, leaves and twigs, powerful and heavily armored for offense and defense, represent a second specialized type. A third is seen in the tapirs, inhabitants of the dense forests and swampy jungle, browsing upon its lush vegetation, excellent at wading and swimming, hiding from their enemies in thicket or stream.

The fossil record of the Perissodactyla is exceptionally complete, and shows that horse, rhinoceros and tapir are three diversely specialized survivors of a large group of animals which were formerly much more abundant and were the principal hoofed animals of the older Tertiary. They included several other specialized groups now extinct, various intermediate types, and the record of all or most of these can be traced back through the Tertiary period, gradually converging into a common primitive stock. From this primitive stock, which appears in

the known record near the beginning of the Tertiary period, can be traced through many successive intermediate stages the evolution of the horse, rhinoceros and tapir, the three surviving specializations, and also the ancestry of the Titanotheres, Chalicotheres, and other specialized types which have become extinct.

This record is derived from the succession of geological formations in the United States and in Europe, and the primitive Perissodactyla appear suddenly in both regions at the beginning of the true Eocene. Presumably they were invaders from some other region, not yet adequately explored by geologists, or in which the geological record has not been preserved. If the former, we may expect to discover the earlier stages of ancestry and to trace back the ancestry of these primitive Perissodactyla to a five-toed stage probably representing the common ancestry of these and other placental mammals. If the latter, the solution of the origin of the higher mammals will remain as it is now, dependent upon anatomical and other indirect evidence.

FOSSIL HORSES OF THE AGE OF MAN

Remains of horses have been found in the surface formations, of Pleistocene age, in all parts of the world. In the recent soils and sediments accumulated during the last few centuries, the bones are mostly those of domestic animals, and are not fossils in the customary sense of the word. They are little if at all altered by petrification, and belong to various breeds of the domesticated horse, *Equus caballus*. They are sometimes of interest to historians, archaeologists, or in researches into the origin of the various breeds of horse.

The Pleistocene horses, prehistoric and much more ancient, were contemporary with primitive man and with the great

Ice Age or Glacial Period. They cover a period from a few thousand years ago to the beginning of the Pleistocene variously estimated from a hundred thousand up to a million or more years old. They are found in all the great continents excepting Australia, and are referred to various species, some still existing, others extinct. In the New World all the fossil horses are extinct, and, in North America at least, appear to be limited to the older part of the Pleistocene; in South America they seem to have survived longer, and are believed by some authorities to have given origin to the herds of wild horses (mustangs) that ranged the Argentine plains as early as the sixteenth century A. D. The more generally accepted conclusion is that the existing wild horses in South America, as in North America, are all "feral," that is to say, escaped from domestication and not truly wild, and that they are the descendants of animals brought over by the Spaniards and other early colonists. They have the characters of the domestic species and interbreed freely with it.

In Africa, on the other hand, the Pleistocene horses have survived to the present day in the various species of zebra, and in the wild ass of Somaliland, the latter the progenitor of the domestic ass. The wild asses of central Asia, belonging to three or more closely allied species or sub-species, are slenderly proportioned, graceful and swift animals quite distinct from either the true horse or the domestic ass. In Central Asia there are also wild true horses, regarded as the probable progenitors of the domestic breeds. The modern horse is regarded by Ewart and others as derived from three distinct strains, one European, inhabiting the northern forests, a second, the steppes of Central Asia and eastern Europe, a third, the plains and deserts of North Africa and

southwestern Asia. Whether these were all derived in turn from a wild species inhabiting Central Asia in the early Pleistocene, and whether they were separately domesticated by different primitive races, or brought with them from their early home in Asia and modified under domestication to suit the environment of forest, steppe and desert, are interesting questions not yet conclusively settled in the present writer's judgment.

All the modern horses, asses and zebras, and all the Pleistocene species of the Old World and North America, are very much alike in teeth and skeleton, so that it has been customary to include them all in the single genus *Equus*. There are considerable differences in size and proportions of the limbs, and more obvious diversity in color and markings of the skin, so that many modern systematists separate the zebras, asses and true horses into different genera. For the palæontologist it is more convenient to retain the old inclusive genus.

In South America, besides the various fossil species of *Equus*, two or more extinct genera of horses are found in the Pleistocene formations. The best known is *Hippidium*, distinguished by a peculiar construction of the nasal bones, certain quite marked differences in the pattern and form of the teeth, and considerably shorter legs and feet. A complete skeleton of this curious horse is in the Museo Nacional of Buenos Aires, casts of it in the American Museum and elsewhere. The purpose of the long slender nasal bones has been variously interpreted; some have thought the animal had a proboscis, others that it had large glands on the face in front of the eyes. More probably it means an extensive soft area behind the nostrils that might perhaps be inflated like the face of the Saiga antelope, and was related to some

kind of specialization of the nasal air-sinuses.

THE TERTIARY ANCESTORS OF THE HORSE

The record of the ancestry of the horse is obtained from the Tertiary formations of various western states. It may be advisable to say a word as to the succession of these formations. They cover wide areas in the western plains from Canada to Texas and in the broad intermontane basins further westward, the strata nearly always lying horizontal and

horse; also corresponding stages leading to the rhinoceros, tapir, camel, deer, dog, cat, and many less familiar animals. Among these ancestral series, none is so extensive or so well documented as the Ancestry of the Horse, and little has been published in regard to the ancestral series of various other animals, which are, for various reasons, less satisfactory for elementary teaching, although equally conclusive to the special student.

The principal stages in the Equidæ evolution are as shown below:

Pleistocene	Glacial and Interglacial	10 <i>Equus</i>
Pliocene	Blanco	9 <i>Platippus</i>
Lower Pliocene or Upper Miocene	Nebraska (Ogallala)	8 <i>Pliohippus</i>
Middle Miocene	Deep River	7 <i>Merychippus</i>
Lower Miocene	Harrison-Rosebud	6 <i>Parahippus</i>
Upper Oligocene	White River { Protoceras beds Oreodon beds Titanotherium }	5 <i>Miohippus</i>
Middle and Lower Oligocene		4 <i>Mesohippus</i>
		3 <i>Epibippus</i>
Upper Eocene	Uinta	2 <i>Orobippus</i>
Middle Eocene	Bridger	1 <i>Eobippus</i>
Lower Eocene	Wasatch	

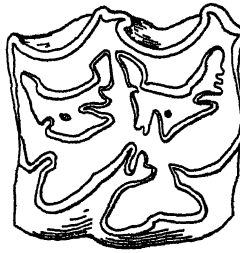
exposed principally in the badlands and escarpments at the sides of the river valleys that traverse these plains and basin regions. Each formation contains its own definite and characteristic fossil mammalian fauna, and the sequence of these faunas is determined beyond cavil by their superposition or overlapping. The entire sequence of faunas has not been found superposed in any one locality; but by correlating the various incomplete series found in different localities the entire series is determined. The details of this correlation are fully set forth in Osborn's Cenozoic Correlation, U. S. G. S. Bull. 361, and in his forthcoming Monograph of the Titanotheriidae, the latter including results of later researches.

In this succession of geological formations are found the remains of a succession of ancestral stages leading up to the modern

Between these principal stages, defined by progressive steps in equine evolution which have generally been admitted by palæontologists as of generic value, might easily be intercalated a series of intermediates, not so well defined or sharply separated. The species of *Equus* from the older Pleistocene, are clearly more primitive in construction of skull and tooth pattern than those of the later Pleistocene and the existing species. The *Pliohippus* from the Lower Pliocene are distinctly nearer to the following stage, *Platippus*; those from the transitional and uppermost Miocene strata are nearer to *Merychippus*, and in fact grade into that genus. In the *Merychippus* stage three sub-stages may be similarly distinguished, in *Parahippus* two, in *Miohippus* and *Mesohippus* two each (though not well separated on the present evidence). In *Orobippus* two



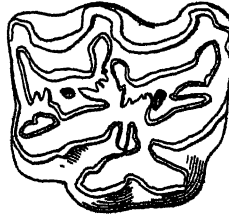
Parabippus
Lower Miocene



Equus caballus
Recent



Miobippus
Upper Oligocene



Equus complicatus
Pleistocene



Mesobippus bairdii
Middle Oligocene



Equus stenensis
Lower Pleistocene



Mesobippus montanensis
Lower Oligocene



Epibippus
Upper Eocene



Pliobippus
Upper Miocene



Orobippus
Middle Eocene



Eobippus
Lower Eocene



Merychippus
Middle Miocene

FIG. 7

FIG. 8

FIG. 7. UPPER MOLARS OF ANCESTORS OF THE HORSE, LOWER EOCENE TO LOWER MIOCENE. SHORT-CROWNED TEETH WITHOUT CEMENT. ALL NATURAL SIZE

FIG. 8. UPPER MOLARS OF ANCESTORS OF THE HORSE, MIDDLE MIOCENE TO RECENT. PROGRESSIVELY LONG-CROWNED TEETH WITH CEMENT INVESTMENT. ALL NATURAL SIZE

stages have been fairly well distinguished. All of the above stages are based on the geological and faunal succession; that is to say, they occur not contemporaneously but in successive geological formations or strata, and associated with correspondingly different faunas. It should be added that in each contemporary fauna there are several species, some more and some less progressive in certain respects or in the sum of their characters; these are not of course regarded as ancestral stages, but as showing the range of variation in the species living at any one time. From this preliminary summary we may turn to a more detailed examination of the facts of our record.

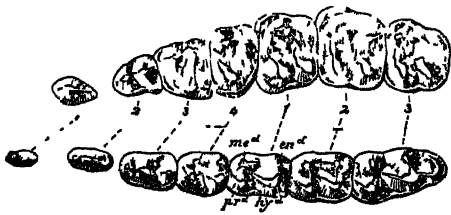


FIG. 9. *Eohippus resartus*. UPPER AND LOWER TEETH, NATURAL SIZE. LOWER EOCENE, BIGHORN BASIN, WYOMING. AFTER OSBORN

Stage 1. *Eohippus*. Lower Eocene. This is the classic Four-Toed Horse. The fore foot has four well developed, usable digits, but curiously enough no trace of the inner digit, or thumb. The hind foot has three well developed digits of subequal size, and small vestigial remains of the first and fifth digits, hardly more than little nodules of bone. The molars are quite short-crowned, with six main cusps partly converted into three crests, an outer crest, an anterior and a posterior inner cross crest, the three crests arranged in a characteristic pattern that suggests the Greek letter π . This pattern is the fundamental pattern of the primitive Perissodactyls. (It is still recognizable in the rhinoceroses, but has

been altered out of all recognition in the modern tapirs and horses. Each phylum in the order has developed its own peculiar type of modification.)

The premolars are smaller than the molars, and of simpler pattern. The first two are simple-crested cutting teeth, the third and fourth have a large inner cusp, and the fourth has the main outer cusp twinned. In addition these two

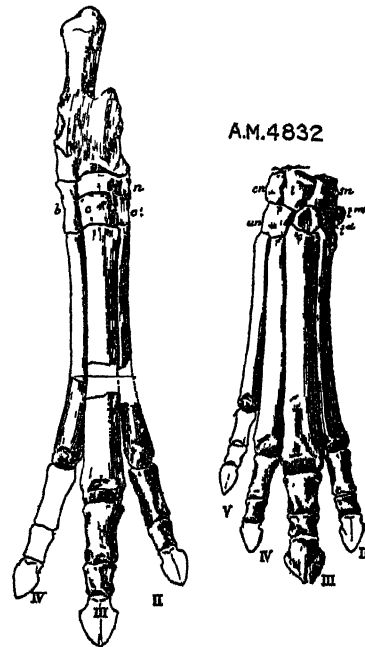


FIG. 10. *Eohippus venticolus*. FORE AND HIND FEET, TWO-THIRDS NATURAL SIZE. WIND RIVER BASIN, WYOMING. FROM THE TYPE SKELETON, REDRAWN AFTER COPE

premolars have rudimentary crests and cusplets which in later stages develop into a molar pattern, so that these teeth in *Eohippus* are on the way to become molariform.

The limbs of *Eohippus* are also very primitive. In the fore limb, the radius and ulna are separate and complete, the shaft of the ulna moderately slender; in the hind limb the tibia and fibula are separate and complete, but the shaft of the fibula quite slender.

Eohippus thus has the normal limb and foot bones of mammals, except for the complete loss of the pollex or thumb, and the almost complete loss of the hallux or great toe and of the outermost digit in the hind foot. The tarsal bones, especially the astragalus, are characteristically Perissodactyl in their form and composition, and, while the ulna and fibula are separate and complete, their articulations are so changed that they permit of only very slight rotation of the foot. The modern tapir tarsus still retains the primitive construction of *Eohippus* little changed; in the rhinoceros it is broadened out, in the horse compacted and shortened.

Eohippus is commonly credited in text-books with a splint of the pollex, as shown in Marsh's drawing of 1876, was republished by Lull in 1907, and copied in various text-books. This is an error. Marsh had only a few fragments of the foot bones, from which he reconstructed the fore and hind feet; unfortunately he mis-identified some of the fragments, and supposed in consequence that there was a facet for a vestigial pollex, which he restored as a splint. The complete skeleton in the Cope Collection (described by Cope in 1885 as *Hyracotherium*), and a number of skeletons more or less complete found since that time, show that no trace of this vestigial pollex is present in any known species of *Eohippus*. Furthermore, in such animals as have a vestigial pollex, it never forms in the course of its reduction a slender, closely appressed splint such as is represented in Marsh's drawing. In all primitive mammals the pollex is sharply offset from the outer digits, affixed to the trapezium by a ball-and-socket joint, and moved by a special set of flexors and extensors, so as to be semi-opposable in the ordinary meaning of the term. This construction is something quite distinct from the merely

divergent digits of many reptiles, and has an important bearing on the primary habitat of mammals.

Mr. J. W. Gidley, in a recent article, has confused the two, and has objected to the term semi-opposable, which however I still think entirely accurate as applied to the condition common to all Paleocene mammals, and one of numerous indications of a primary arboreal adaptation. The evidence to this effect will be published later in a memoir on the Paleocene mammalian faunas of New Mexico.

Thirteen species of *Eohippus* have been described, varying in size from that of a cat to a fox-terrier. Most of the material is fragmentary, jaws, parts of jaws and teeth, but three fairly complete skeletons are in the American Museum, one in the Amherst Museum. Many thousands of jaws and jaw-fragments have been obtained in the Lower Eocene of Wyoming and New Mexico, a few from Utah. The Lower Eocene of England, Belgium and France has also yielded a few specimens, the best a fairly good skull, described under the name of *Hyracotherium*, a name older than the more appropriate *Eohippus*, and hardly separable from it.

It is quite possible that certain species of *Eohippus*, when more intensively studied, will appear to be more directly in the line of ancestry of the horse, others of the tapir or rhinoceros or of some of the extinct phyla of Perissodactyls. A closely related genus, *Homogalax* ('*Systemodon*'), has been regarded as ancestral to the tapirs. This appears improbable in view of recent studies and of new evidence from the Mongolian Eocene; its relationships are rather with the Lophiodonts. In any event it is very close to *Eohippus*, and the feet are not distinguishable except by size, and absence of the vestigial first and fifth digits on the pes.

The American specimens of *Eohippus* come from various levels in the Lower Eocene strata, and one might expect to find progressive modification shown in the teeth from lower to upper levels, as is shown in a number of other contemporary mammalian phyla. Careful study, however, has failed to detect such evolutionary change, which would serve as a guide to the probable character of the next older stage in equine ancestry. *Eohippus* appears quite suddenly, in great numbers, at a particular level in the Wasatch formation, and was evidently an invading type, for nothing in the fauna of the underlying strata can be regarded as ancestral.

There is little doubt, however, that the ancestor of *Eohippus* is to be sought

Museum, a finely preserved skull and fore foot in the Yale Museum, but otherwise it is known only from jaws and fragments. These represent a number of species, some nearer to *Eohippus*, some more advanced in tooth characters, but with about the same range in size. The fore foot differs from *Eohippus* in slightly larger size of the central digit, the hind foot in the disappearance of the vestigial first and fifth digits, while in the teeth the molar crests are somewhat more pronounced and the third and fourth premolars have become more like the molars in pattern and size. The more primitive species of *Orohippus* are found only in the lower part of the Bridger formation, the more advanced species in the upper part, so that here we

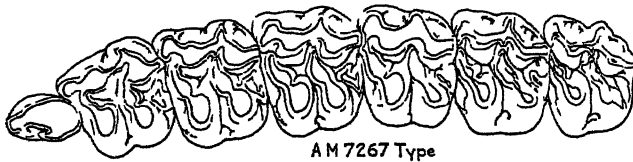


FIG. 11. *MIOHIPPIUS QUARTUS*. UPPER TEETH, NATURAL SIZE. JOHN DAY BASIN, OREGON. AFTER OSBORN

amongst the Condylarthra, primitive five-toed ungulates of which *Phenacodus*, a contemporary of *Eohippus*, is the best known form. Probably the earlier stages in the evolution of the horse will be found, if at all, in the Paleocene and late Cretaceous Condylarths of some intermediate northern region whence came the American *Eohippus* and European *Hyracotherium*. Central or northern Asia is the region indicated, but thus far no such animals have been found. The negative evidence from a few preliminary explorations has, however, no great weight, save to indicate that northern rather than Central Asia was the center of origin of the family.

2. *Orohippus*, the second stage in the evolution of the horse, is found in the Middle Eocene Bridger formation. One nearly complete skeleton is in the American

do have a progressive evolution in the species.

3. *Epihippus*, the third stage in equine evolution, is imperfectly known. No complete skulls or skeletons have yet been found, but a large number of upper and lower jaws and various fragmentary skeletons with the fore and hind feet preserved in some of them. It carries on the line a step further in the somewhat higher-crowned and more sharply crested molars, the two posterior premolars are almost exactly like the molars in pattern, the central digit in both fore and hind foot is relatively larger, the fifth toe of the fore foot is smaller and more slender, although still a complete and usable toe. Its remains have been found in the Upper Eocene Uinta formation of Utah. The specimens are principally in the American

Museum, Yale, Princeton and Carnegie Museums.

4. *Mesobippus*, the fourth stage, is found in the Lower and Middle Oligocene formations of the western plains region from Saskatchewan to Colorado. Numerous skulls and many complete skeletons are known, and many thousands of jaws, feet and other fragments. There are various species, all much alike, and about the

side toes much smaller than the central one, although they are complete and reach the ground in an ordinary step. Of the outer digit in the fore foot, complete in *Epibippus*, only a very short, small splint remains, hardly more than a nodule of bone. The shaft of the ulna, although still complete, is reduced to a thin, slender,

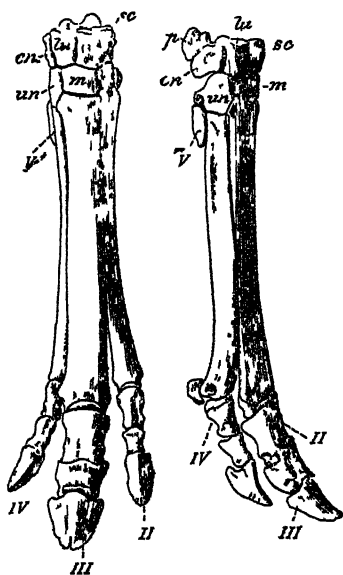


FIG. 12. *MIOHIPPIUS INTERMEDIUS*. FORE FOOT, ONE-THIRD NATURAL SIZE. UPPER OLIGOCENE, SOUTH DAKOTA. FROM THE TYPE SKELETON, AFTER OSBORN AND WORTMAN

size of a prairie wolf. It is a considerable step forward from *Epibippus*, and not quite in the line of trend indicated by the three Eocene stages. Three of the premolars are molariform, so completely so that they are not easily distinguished from the molars, and are slightly larger. The first premolar (p_1^I) remains small and simple, tending rather to disappearance. The fore and hind feet are three-toed, the

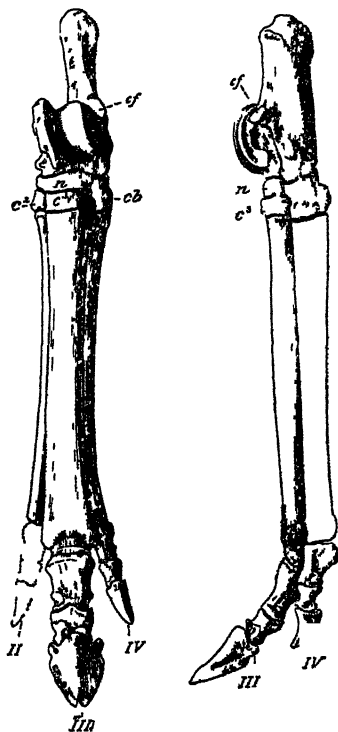


FIG. 13. *MIOHIPPIUS INTERMEDIUS*. HIND FOOT, ONE-THIRD NATURAL SIZE. UPPER OLIGOCENE, SOUTH DAKOTA. FROM THE TYPE SKELETON, AFTER OSBORN AND WORTMAN

The drawing is incorrect in failing to show the cuboid facet on metatarsal III, quite distinct on the original.

flattened rod, lying close to the back of the radius, although not co-ossified with it. The distal end of the bone is very apt to be co-ossified. The shaft of the fibula is still further reduced to a long delicate sliver of bone, the lower part lying against the tibia and partly co-ossified with it.

There is a considerable gap between

Epibippus and *Mesobippus*, which may be partly filled when we know more specimens and species of *Epibippus*, and have a better idea of its range and characters. The Lower Oligocene species of *Mesobippus* are also incompletely known, although they appear to be very close to the well known species of the Middle Oligocene. Even allowing for this imperfect acquaintance with the adjacent species of the two stages, it is a wider break than one would expect from the relations of the Uinta and Chadron formations in which they respectively occur. I believe that *Mesobippus* is not directly descended from *Epibippus*, but from an unknown related genus, more progressive, and inhabiting

metatarsal supports only the ecto-cuneiform bone of the tarsus; the cuboid and the inner cuneiform are wholly supported on the lateral digits as in all the earlier types. In *Mesobippus* the cuboid has gained a footing on the central metatarsal, as in all the later horses. This is a mechanical advantage in the reduction of the lateral digits, giving the tarsus a more solid support on the central digit, that keeps it from "rocking." We shall see that at a later stage the inner cuneiform also acquires a footing on the central metatarsal or cannon bone. (Marsh's drawings of the hind feet of *Mesobippus* and *Mesobippus* do not correctly represent the normal tarso-metatarsal relations).

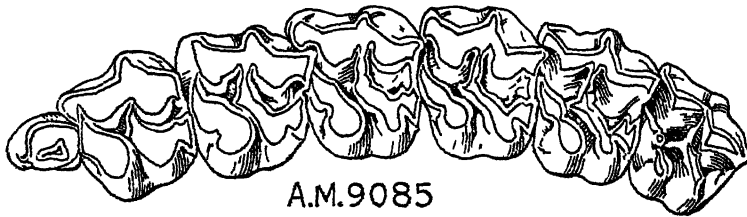


FIG. 14. *PARAHIPPUS PAWNIENSIS*. UPPER TEETH, NATURAL SIZE. LOWER MIOCENE, SOUTH DAKOTA

perhaps a more northerly part of North America.

5. *Mesobippus*, the next stage, is Upper Oligocene, and very closely related to *Mesobippus*, so that it is doubtful whether the two genera should be kept separate. Except that the species average larger in size, it can hardly be said to be more progressive. Marsh's classic diagram of 1892, which was republished by Lull in 1907, and copied in various text-books, represents the splint of the fifth digit as more reduced than in *Mesobippus*, but this does not seem to be the case. There is, however, one progressive step, not noticed by Marsh, and not invariable or constant, that generally distinguishes *Mesobippus*. In the hind foot of *Mesobippus* the central

The side toes in *Mesobippus* and *Mesobippus* are much reduced, but they still reach the ground and help to support the limb. This is partly because of the unusual shortness of the phalanges, or toes proper. This proportion is rapidly and progressively changed in the next stage in the direct line, but is continued for some time in the *Hypobippus* side branch.

6. *Parahippus*, the sixth stage, is found principally in the Lower Miocene formations over a much wider area, from Montana to Texas, and many skulls and incomplete skeletons are known. The various species cover a very considerable range in size and advance in structure, some not easily distinguished from *Mesobippus*, while others are hardly separable

from *Merychippus* of the Middle Miocene. The older species geologically are more primitive, and the later species more progressive in general, but there is no uniform progress among them, some being more advanced in size, some in structure

The tooth pattern changes by the progressive conversion of the two transverse crests into a pair of crescents at first oblique, tending to become antero-posterior in direction, while the inner pillars of the crests, especially the anterior one, be-

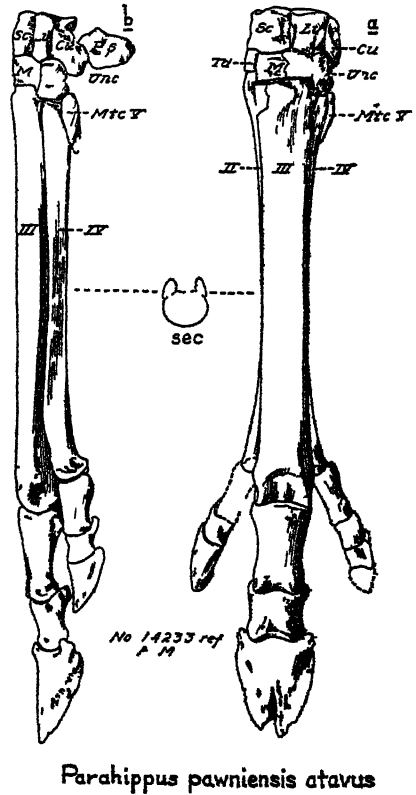
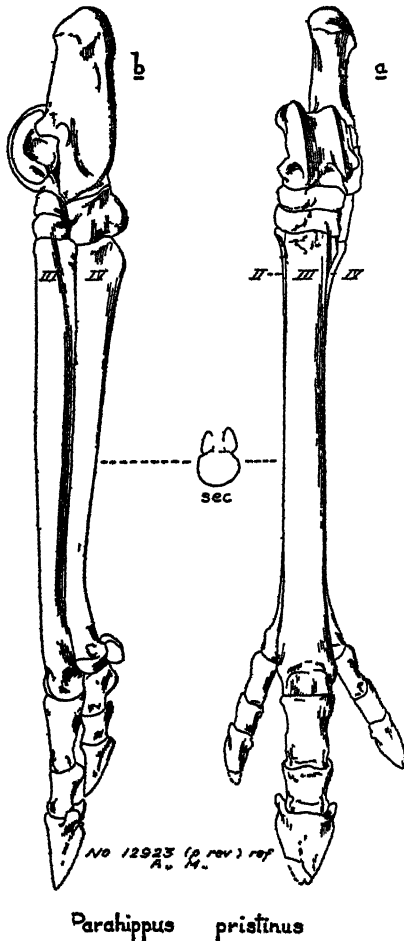


FIG. 15. FORE AND HIND FEET OF PARAHIPPUS, TWO-FIFTHS NATURAL SIZE. LOWER MIOCENE, SOUTH DAKOTA. AFTER OSBORN

of the teeth, some in structure of the feet. They suggest a group of related species of high individual variability with perhaps a good deal of hybridizing among different races. The result, however caused, is a rapid advance of the race during the Lower Miocene.

come more or less separated. This change is continued and completed in the various species of *Merychippus*. At the same time the valleys between the crests begin to fill up with a new structure the *cement*, formed primarily as a deposit of "tartar" on the crown and during the period that

the tooth is emerging from the jaw. The cement in *Parahippus* is usually a rather thin coating, sometimes more considerable; in some of the latest and most progressive species it completely fills the valleys and invests the outside of the crown as in *Merychippus*.

The feet are equally variable. The side toes are sometimes almost as large as in *Miobippus*, the phalanges almost or quite as short. Other species have the lateral digits much reduced, so that the shafts of their metapodials are no larger than a match. The vestigial fifth digit varies from a very short small splint to a tiny nodule of bone. The shaft of the ulna is reduced to a slender flattened rod plastered against the back of the radius, but still separate from it.

The permanent teeth are heavily coated with cement, which fills the valleys and invests the outside, so that in wear the enamel is everywhere supported on one side by cement, on the other by dentine, and as in modern horses makes a ridge on the grinding surface that is continually renewed. The cement is deposited at a later stage in the growth of the teeth than in the modern horses. It begins to be deposited as the tooth comes close to the bony surface of the jaw, and is completed as it cuts the gums. The milk teeth have very little cement on them, also late deposited.

The feet have always a long, relatively cylindrical cannon bone, longer phalanges, and more convex hoofs in comparison with *Miobippus*, approaching the smaller



FIG. 16. *MERYCHIPPUS PANIENSIS*. UPPER TEETH, TWO-THIRDS NATURAL SIZE. MIDDLE MIOCENE, WESTERN NEBRASKA

7. *Merychippus*, the seventh stage, appears in the Middle Miocene, and is very common in the later Miocene formations. It is especially distinguished by the rapid elongation of the cheek teeth. In the earliest species the upper molars are about as high as they are wide; in the latest and most progressive species they are from two to two and a half times as high. The milk teeth are short-crowned, as one would expect of milk teeth, but are disproportionately so, and their pattern is decidedly archaic, very like that of *Parahippus*. The permanent molars and premolars have the pattern converted into a pair of outer crescents, a pair of inner crescents and a pair of inner pillars, the anterior one more or less separated in different species.

modern species of horses (ass, kiang, etc.) in proportions. The side toes, however, are always complete, although slender and shortened up so that they do not reach the ground in an ordinary step, but are like the "dew claws" of various modern animals.

The shaft of the ulna is always co-ossified with the back of the radius in adult *Merychippus*, separate in the colts.

Twenty-five species of *Merychippus* have been described, many of them probably invalid or sub-species, but the genus is very wide-spread and abundant, and covers a considerable range of variation. It is found from Florida, Texas and California to Montana and Oregon.

In many species of *Merychippus* there is a marked hollow or fossa upon the side

of the face in front of the orbit. It is sometimes broad and shallow, sometimes deep and more or less restricted into a deep pocket, and frequently divided more or less clearly into two pockets, the

authorities have thought that they were analogous to the lachrymal fossae on the face of ruminants, lodging a scent-gland; others have seen analogies to the pockets that lodge the proboscis muscles of the

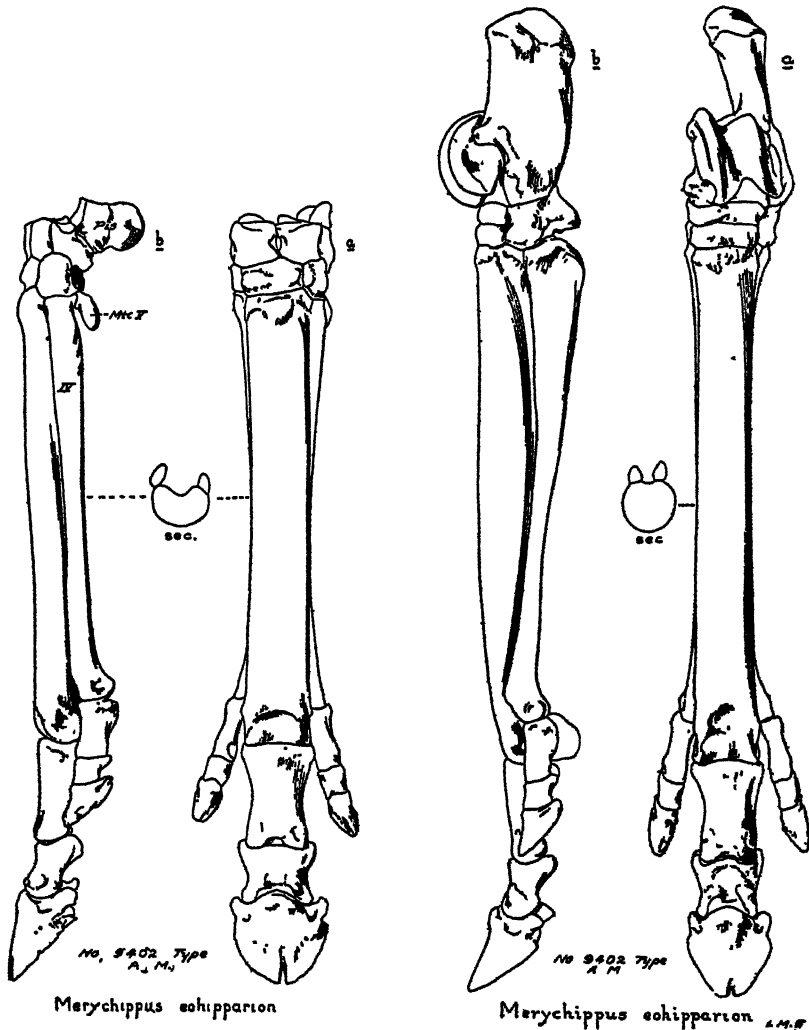


FIG. 17. *MERYCHIPPUS SCHIPPARION*. FORE AND HIND FEET, ONE-THIRD NATURAL SIZE. MIDDLE MIOCENE, COLORADO. AFTER OSBORN

lachrymal and malar fossae. One or both of these fossae are retained in many species of the later horses, but they have completely disappeared in *Equus*. Their significance has been disputed; some

tapir. It seems more probable however that they lodged an enlarged diverticulum or extension of the small blind sac that opens just within the nostrils of the modern horse; but the functions of such

an organ have not been made clear. The writer regards the appearance of these fossae as primarily conditioned by certain mechanical needs in bracing a progressively enlarging skull; and that the spaces later required for the elongated teeth and extension of the internal nares bones, might well be occupied in the meantime by diverticula of unknown but perhaps not very essential function,

which disappeared as the space was required for more important uses. The very variable occurrence of the fossae in the different species is difficult to reconcile with their serving any very essential functional purpose. (See Gregory, 1920 Bull. Am. Mus. Nat. Hist., vol. xlii, pp. 265-284; Boule, 1920, Mam. Foss. de Tarija, pp. 106-110; Studer, 1910, Lydekker, 1893.)

Geological distribution of later tertiary equids in Europe and North America

EPOCHS AND STAGES		AMERICAN FORMATIONS AND GENERIC ZONES		OCCURRENCE OF EQUID GENERA		
				Europe	North America	
MIOCENE	Pliocene	Plaisancian	Blanco	HIPPARION	<i>Hipparion</i> . Specialized aberrant species	<i>Plisippus</i> <i>Hipparion</i> . Specialized aberrant species
		Pontian	Republican			<i>Pliohippus</i> } <i>Protobippus</i> } more advanced species <i>Hipparion</i> }
			Valentine	MERYCHIPPUS	<i>Anchitherium</i>	<i>Pliohippus</i> } Primitive species close to <i>Protobippus</i> } <i>Merychippus</i> <i>Hipparion</i> }
		Sarmatian	Santa Fé			<i>Merychippus</i> . Advanced species pas- sing into the three later genera.
		Tortonian	Pawnee Cr'k.			<i>Merychippus</i> . Most larger species, fore- casting the three later genera.
		Helvetian	Mascall L'r. Sheep Cr'k.			<i>Merychippus</i> . Small, primitive, wide individual variation, which fore- casts the species of the following stage
			Upper Harrison Upper Rosebud			<i>Parahippus</i> . Widely varying distinct species, mostly progressive in one or more features, some approaching <i>Merychippus</i>
		Burdigalian	L'r. Harrison	<i>Parahippus</i> . Larger and smaller spe- cies, rather primitive		
			Lower Rosebud Monroe Cr'k.	<i>Parahippus</i> . Small primitive species. <i>Miohippus</i> . Mostly large and spe- cialized species		
		Aquitanian	John Day	MIOHIPPIUS	No Equida	<i>Miohippus</i> . Larger and smaller species

The geologic occurrence of *Merychippus* is in the middle and upper Miocene "Merychippus Stage." The first appearance is in the Lower Sheep Creek Beds (Zone) and equivalents, with small primitive species; in the next following Pawnee Creek Beds are larger and more progressive species, and in the Santa Fé beds species hardly separable from the following genera *Protobippus*, *Pliobippus* and *Hipparion*, and mingled with others that must be referred to these genera. A few species of *Merychippus* linger in the Republican beds, then they disappear.

8. *Pliobippus*, the eighth stage, is a direct outcome of one of the species groups of

less than the size of the ass to equal to a small domestic horse. The fossæ, or pockets on the sides of the face in front of the orbits, are deep and extensive in all the older known species, shallow in some later species.

The proportions of the feet are more robust and heavier than in *Merychippus*, averaging about as in the modern Kiang; the larger and more progressive species have stouter limb and cannon bones. The inner cuneiform has shifted over to acquire a footing on the cannon bone, a progressive character earlier acquired by the *Hypobippus* side branch, but appearing here for the first time in the direct line.



FIG. 18. *PLIOHIPPIUS LEIDYANUS*. UPPER AND LOWER TEETH, TWO-THIRDS NATURAL SIZE. FROM THE SKELETON, UPPERMOST MIOCENE, NEBRASKA. AFTER OSBORN

Merychippus (*M. campestris* and allies), and is at first difficultly separable from *Merychippus*. The teeth become progressively longer, but retain the transverse width, simple lines of enamel surrounding the "lake borders," strong inward curvature and close union of inner pillars with inner crescents. The genus is more readily distinguished by its milk teeth, which are much higher-crowned (one and a half times to twice as high) as in *Merychippus*, a fourth to a third narrower transversely, and quite heavily cement-coated, as in modern horses.

The skull is large in proportion to the skeleton, different species varying from

The footing is not so broad and solid as in the Pleistocene and modern horses. It is not conditioned by the reduction of the lateral digits, for it occurs in *Hypobippus*, and in a species of *Pliobippus* in which these are still complete. Nor by robust proportions or size, since it occurs in the very small and extremely slender species of *Hipparion* from the middle Pliocene of Florida and Texas, also in all the Old World *Hipparions*, but not in most of the American species of this genus.

Pliobippus is said to be one-toed, and without question the lateral phalanges were greatly reduced or totally absent in some species. No adult specimens, how-

ever, show any of the lateral metapodials complete down to the expanded knob or plate which represents the distal end of the complete bone, and, in a juvenile skeleton described by Troxell as monodactyl, the form of the tip is certainly not that of a completely calcified end, so that it is doubtful whether bony pha-

dition as the teeth in *Parahippus*; some species had side toes and others did not, but there was a general reduction of the laterals and advance of the foot bones in all details in the direction of *Equus*

9 *Plesippus*, the ninth stage, is known from the late Pliocene of Texas and California, but until 1924 so imperfectly

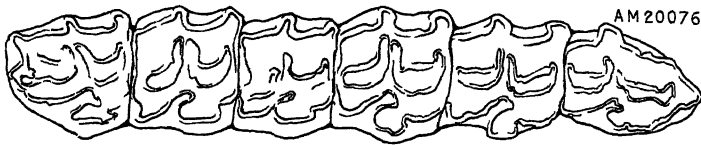


FIG. 19. *Plesippus simplicidens*. UPPER TEETH, ONE-HALF NATURAL SIZE FROM A SKELETON, MIDDLE PLIOCENE, TEXAS



FIG. 20. *Plesippus* SKULL FROM MIDDLE PLIOCENE OF TEXAS, COMPARED WITH MODERN EQUUS SKULL. ONE HALF NATURAL SIZE

langes would not have calcified before the animal became adult. On the other hand, in at least one species of *Pliohippus* from Texas, perfectly typical as respects its skull and teeth, the lateral digits have a complete set of phalanges, proportioned as in an average *Merychippus*. On the whole it seems probable that the toes in *Pliohippus* were in the same unstable con-

(a few teeth only) that it could not be characterized and distinguished as a separate generic stage. In 1924 Mr. George Simpson and I found two skeletons at Mount Blanco, Texas, that between them give almost every detail of the anatomy. The animal compares in size and most proportions with the Arab horse, but the hoofs are much smaller, the back

shorter and the barrel less rounded and convex

The teeth are like those of *Pliobippus* in pattern, but with longer crowns, much less curved (as in *Equus*); the pattern in various details makes some approach to

however in a thin flattened and expanded sliver instead of the little knob of *Equus*. They are slightly longer. The vestigial fifth metacarpal is retained on the outer side of the fore foot, and the trapezium on the inner side, as tiny nodules of bone,



FIG. 21. PLESIPPUS FORE AND HIND FEET (PHOTO), FROM SKELETON MIDDLE PLIOCENE, TEXAS. SHOWING VESTIGES OF FIFTH DIGIT AND TRAPEZIUM

Equus, but on the whole the tooth characters come nearer to *Pliobippus*.

The feet on the other hand are very much like those of *Equus* in proportions and general appearance. The lateral digits are reduced to splints, which end

relatively smaller than in *Merychippus* and *Pliobippus*. In *Equus* these bones are occasionally calcified, but not normally present.

The fibula is reduced to a splint which in *Plesippus* is distinctly shorter than in

any species of *Equus*. Probably this is a variable non-adaptive character in the later Equidæ; it is as far advanced in *Merychippus* as in *Equus*, further advanced in *Plesippus* and in some species at least of *Hipparion*.

The skull of *Plesippus* is remarkably *Equus*-like in size and proportions. It has acquired the long straight lines of the face, as opposed to the shorter proportions and more convex outlines of the head in the older Equines. It has almost completely lost the deep facial pockets of *Pliobippus*; only slight shallow hollows remain.

10. *Equus*. Pleistocene to Recent. The earliest certain recorded appearance of *Equus* proper is at the base of the Pleistocene in America and Europe. *Equus steno-*

The few that are known from skulls and skeletons are distinct species, but not widely different from *E. caballus*.

Equus is a cosmopolitan genus, and has been found fossil in all parts of South America, in North America (except within the glaciated area), in practically all countries of Europe and Asia, in Africa from Algeria to Natal, failing to reach Australia and the islands that lie beyond the limits of the continental shelf.

DIVERGENT LINES OF EQUIDÆ

In the preceding pages the direct line of succession leading from *Eobippus* to the modern horse has been described. There are also a number of side branches, more or less closely related. The living zebras and asses, although different in color-



FIG. 22. *EQUUS* SP UPPER TEETH, ONE-HALF NATURAL SIZE LOWER PLEISTOCENE, NEBRASKA

mus of the Arno valley in Italy is a rather small species, primitive in the tooth construction, and nearer to *Plesippus* in this and other details than are the later species. Still it has the characteristics of *Equus* in the anterior inner pillar of the upper molars, flattened, with a narrow much constricted commissure connecting it with the anterior inner crescent, while the posterior inner pillar is reduced and tends to merge into the posterior crescent. The classic Val d'Arno and Asti fossil mammals have been generally called Upper Pliocene. According to the more recent correlation they are Lower Pleistocene. The older Pleistocene formations in North America contain remains of various species of the genus. Some are apparently as primitive as *Equus stenonius*, others as advanced in teeth as the modern horse.

pattern, size and proportions, are so close to the domestic horse in skeleton that it is very difficult to distinguish their fossil remains. Some of the extinct species of *Equus* are thought to be especially related in teeth to the zebra, others are more certainly related to the ass; but the three types are not clearly distinct among the Pleistocene species.

Hipparion is a classic genus of the Pliocene of the Old and New World. It is distinguished from *Equus* by the separate protocone of the upper molars. A dozen or more valid species are known, three or four from the Pliocene, and uppermost Miocene of Europe, Asia and Africa, the rest from North America. All in which the skeleton is known retain complete lateral digits.

The species range from the size and

proportions of an ass down to those of a dorcas gazelle, and have a wide range also in the construction and proportions of the teeth. In some species the enamel of the lake borders is thrown into much more complex folds than in the horse, in others it is simpler. In some the protocone is round oval as in *Merychippus*, in others (subgenus *Neohipparion*) flattened as in *Equus*. One group of small American species (new subgenus *Nannippus*) has the teeth very long-crowned, up to a fourth longer than in any living horse; oval protocones and extremely slender limbs and feet, in which the side toes are complete but no trace remains of the fifth digit and trapezium. This group is typified by *Hipparion phlegon* of the Blanco formation, of which I secured skulls,

They have in common the separate protocone and usually, if not always, the retention of the lateral digits. (The first is essentially a primitive character because it is caused by the commissure or connecting crest between protocone and protoloph remaining low or short, while the rest of the crown is elongating. It would seem to be a mechanical defect, making it easy for the protocone to break away from the rest of the tooth, except for the heavy coat of cement; but it is not a defect, for it did not prevent certain species from surpassing the horse in length of the teeth. Upgrowth of this commissure would convert the tooth in certain species into an *Equus* tooth, loss of the lateral digits into an *Equus* foot.)

The various American species grade

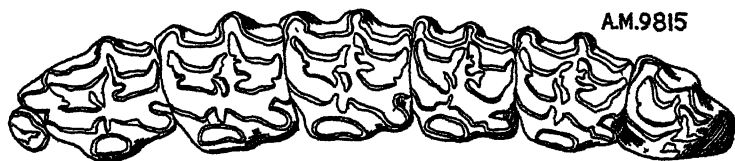


FIG. 23. *HIPPARION WHITNEYI*. UPPER TEETH, TWO-THIRDS NATURAL SIZE. FROM A SKELETON, UPPER MIOCENE, SOUTH DAKOTA

feet etc. in 1924. Contrast it with the contemporary *Plesippus*, with stout limb and foot bones, the side toes reduced to splints but the trapezium and fifth digit still retained. Another group, mostly Old World species, typified by the well known *Hipparion gracile* of Pikermi and Samos, is comparatively large and robust with relatively stout limbs and feet and the side toes larger than they are in *Merychippus*. Most of the species have the lachrymal fossa in the side of the face deep and well defined, but in some it has disappeared almost completely.

The various species of *Hipparion* seem to have been trying out a variety of combinations of progressive features, carrying some of them further than *Equus* has done.

back into *Merychippus*, from which *Hipparion* is clearly derived. In the Old World it appears as an invading type at the end of the Miocene (Pontian fauna).

Hippidium, a small group of South American horses, has exceptionally short legs, a curiously constructed nasal region in the skull, and teeth much like those of *Pliohippus*. They are of about the same bulk as the true horse. The free portion of the nasal bones is very long and slender, the notch between them and the maxillary bones extending far backward. This indicates I believe, not a proboscis as supposed by some writers, but a soft flexible structure behind the nostrils, prevented from collapsing by the slender nasal bone. Possibly it was analogous

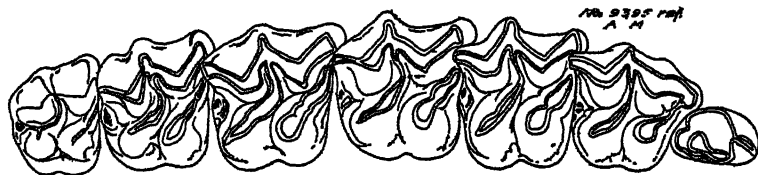
to the curious face of the Saiga antelope, but its purpose and exact character are unknown. These animals, evidently descended from *Pliobippus* of the North American Pliocene, are known only in South America in the Pleistocene. The short legs were perhaps an adaptation to mountain habitat. Another South American Pleistocene genus, *Onobippidium*, has deep fossae or pockets in the side of the face in front of the orbits, as in many species of *Merychippus*, *Pliobippus* and *Hipparion*. It is otherwise much like *Hippidium* and probably of similar habits. *Hyperbippidium* or *Parabhipparion* is even shorter legged and otherwise similar.

Anchitherium and *Hypobippus*. An older side branch is represented by a series of

apparently to forest life judging from its associations. These animals were larger than the contemporary stages of true equines, the last of them (*H. matthewi*) nearly as large as a modern horse.

This line invaded the Old World at the beginning of the Miocene, and is found in the Miocene formations of Europe and Asia until the end of the Miocene or beginning of the Pliocene. The name *Anchitherium* was given by Meyer to the European species, described nearly a century ago; and at one time, before the American Tertiary equines were known, *Anchitherium* was supposed to be in the direct ancestral line of the horse, linking it with *Palaeotherium*.

Archaeobippus. Closely related to *Para-*



Hypobippus osborni

FIG. 24. *HYPOBIPPUS OSBORNII*. UPPER TEETH, TWO-THIRDS NATURAL SIZE. MIDDLE MIOCENE OF COLORADO. AFTER OSBORN

species that begin in the Upper Oligocene with certain species of *Miobippus*, are continued by the Lower Miocene *Kalobassippus* and by *Hypobippus* of the later Miocene surviving to Lower Pliocene. This series retains the more primitive construction of the teeth with oblique crests and outer crescents, lengthening out crowns a little, and to some extent paralleling the rhinoceros adaptation of grinding teeth. The side toes also are persistently primitive, reduced progressively but more slowly than in the typical equines, and the hoofs are relatively large and splayed. Professor Osborn has designated this as the Forest Horse, and its adaptation is clearly to softer ground and more succulent food, although not

bippus, and like it derived from *Miobippus*, this line remained small, short-crowned, and almost unchanged except for elongated face and deep facial fossae. It is found in the Miocene. The skeleton so far as known is like that of the smaller species of *Parabhippus*, of which it may be considered a subgenus.

DIVERGENT LINES LEADING TO TAPIR, RHINOCEROS AND OTHER TYPES

In the preceding pages have been reviewed a series of successive stages leading up from the little four-toed *Eobippus* to the modern horse. Each stage is found in its appropriate position in the geologic succession, never below or above its proper level (except for one or two

unaltered survivals noted in the review and now extinct have also been reviewed. indicated in the diagrams). A number of We have now to review various races re-

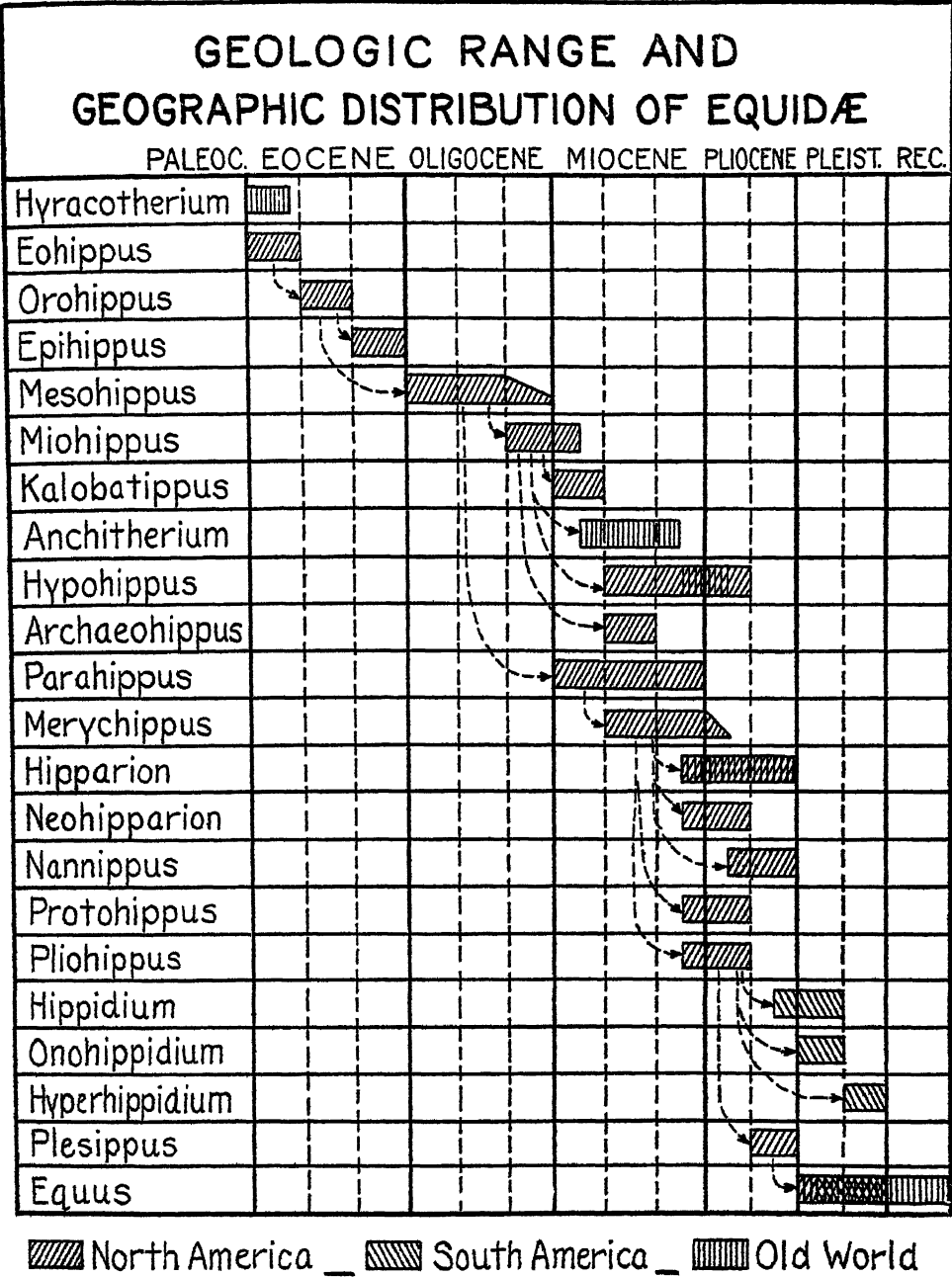


FIG. 25

side branches leading up in similar manner to aberrant specialized Equidæ types

lated to the horses but not included in the family, leading up in quite similar

fashion to a variety of specialized types, some living, others extinct, widely diverse from horses in appearance, yet with certain underlying identities in skeleton structure that enable them to be grouped under the order Perissodactyla.

The surviving types are the tapirs and the rhinoceroses. The extinct types are the Titanotheres, the Chalicotheres, the Palæotheres, Colodonts, Lophiodonts and a variety of minor side branches. Each of these types is shown by the fossil record to be derived from animals practically identical with *Eohippus* progressively divergent into their final or existing special form. The ancestral series are none of them so extended, complete and clearly defined as that of the horse nor has so much been done toward securing and studying adequate collections. Nevertheless they are clear enough in their general lines, and where they have been studied intensively they show similarly exact series in successive geological formations.

The rhinoceros, tapir and colodont lines are not clearly distinguished in the Lower Eocene. In the Middle Eocene the rhinoceros ancestry is first clearly distinguished in *Hyrachyus*. This animal, about the size of a wolf, has taken on the broader lines of construction of the cheek teeth of the rhinoceroses, but is still short-crowned like all the Lower Eocene Perissodactyls, and the front teeth retain the primitive cropping type from which the horses have not changed greatly. The feet are like those of *Eohippus*, four toes in front and three behind. In the Oligocene the rhinoceroses are more various in type and include larger animals. The Amynodonts retain four toes in the fore foot and convert the canine teeth into large tusks. The Hyracodonts reduce the toes to three on each foot, and like the horses begin to lengthen out the

foot and reduce the side toes, also lengthening the crowns of the cheek teeth, but retaining the cropping front teeth. The true rhinoceroses convert a pair of incisors, above and below, into tusks, and the other front teeth progressively degenerate and disappear; they lose the outer digit of the fore foot by progressive stages, but instead of lengthening the limb and foot they broaden it with increase in size. About the end of the Oligocene, Hyracodonts and Amynodonts disappear and the true rhinoceroses begin experimenting on horns, first a pair of little nubs on the tip of the nasal bones, then in the Miocene and later Tertiary they try out a single nasal horn, a horn just back of the tip of the nasal, two horns arranged tandem, and a single horn on the frontal bone. They split up into a number of rather closely related parallel races, most of them increasing to more or less gigantic size and massive proportions. The African rhinoceroses with two horns have specialized further in the loss of the front teeth, and one of them, the White Rhinoceros, has high-crowned teeth of a peculiar pattern. The Woolly Rhinoceros of Siberia, although older than this existing species, has carried its trend of specialization further in a longer and heavier front horn and a bony crest between the nostrils underneath it which serves to brace it solidly.

The tapir line is rather doubtfully identified in the Eocene, but in the Oligocene and later horizons it is represented by a well recognized approximate series, mostly of Old World species. Few fossil specimens have been found in the New World, yet enough to show that they inhabited North America.

Tapirs retain the four toes in the front foot and three in the hind foot of the early Eocene Perissodactyls, and in many features of skeleton and teeth are very primi-

tive. The cropping incisors are retained, and the cheek teeth are still short-crowned, but the premolars are completely molariform, and the pattern of the molars altered to transverse chopping crests, the ectoloph almost disappeared. The progressive molarization of the premolars can be traced in the tapir stages from Oligocene to Pleistocene just as it can in the Eocene horse stages. One remarkable character is the evolution of a proboscis, also partly traceable in the Oligocene-Recent series.

The Titanotheres are an early extinct family of the Perissodactyls which specialized in giant size, retaining the four-three toes, developing massive rhinoceros-like proportions, a pair of long "horns" on the front of the skull, converting the molar pattern into two outer crescents and an inner pair of rounded cusps, the front teeth degenerating. These are common in the American Eocene and Lower Oligocene, and their evolution has been studied by Osborn from a splendid series of skulls and skeletons. The earliest stage, *Lambdaotherium*, is closely related to the somewhat older *Eobippus*, and must have been derived from a predecessor which would be still nearer, but has not yet been discovered.

(Students of phylogeny whose attention has been concentrated upon the *differences* that will enable them to distinguish one stock from another in the early stages of their differentiation, may take exception to the above statement. A fair and honest appraisal of the characters of *Lambdaotherium* as compared with *Eobippus* on one hand, and *Titanotherium* on the other, fully warrants the statement. I regard the over-emphasis of such differences, on account of their real or supposed phyletic importance, as gravely misleading.)

Intermediate between Titanotheres and

horses are the Palæotheres of the Old World Eocene, much like the early equines in teeth, but robust and massive, with a tendency to develop a proboscis.

Another remarkable series of extinct Perissodactyls is the Chalicotheres, which in the teeth are very like Titanotheres, the skull and neck take on more the proportions of a horse, the body those of a tapir, while the limbs and feet suggest rhinoceroses except that they have large claws instead of hoofs on the toes. These have a record lasting from the early Oligocene to the Pleistocene, and a doubtful Middle Eocene ancestor of more primitive type with only the obscure beginnings of the various peculiarities of the race.

The Colodonts, related to the tapirs, and like them with a tendency to develop a proboscis, but with slender limbs and progressive elongation of the foot and reduction of the toes in some genera to three on each foot, are a group very imperfectly known or studied as yet. Another extinct group, the Lophiodonts, appears to be related on one side to the Colodonts, on the other to the Eocene rhinoceroses. Both groups are in need of further critical research in the light of recent discoveries, especially of Mongolian Eocene Perissodactyls.

In general it would appear that the Perissodactyls start in the early Eocene with a great number of closely related stocks, which specialize progressively in the successive Eocene horizons, partly on parallel, partly on divergent lines. These numerous branches are reduced by extinction one after another of most of the intermediate and competing lines, while the survivors became more and more divergent and specially adapted to their diverse modes of life. One branch may give rise to side specializations paralleling other branches, as the Hyracodont rhinoceroses and the Colodont tapirs parallel

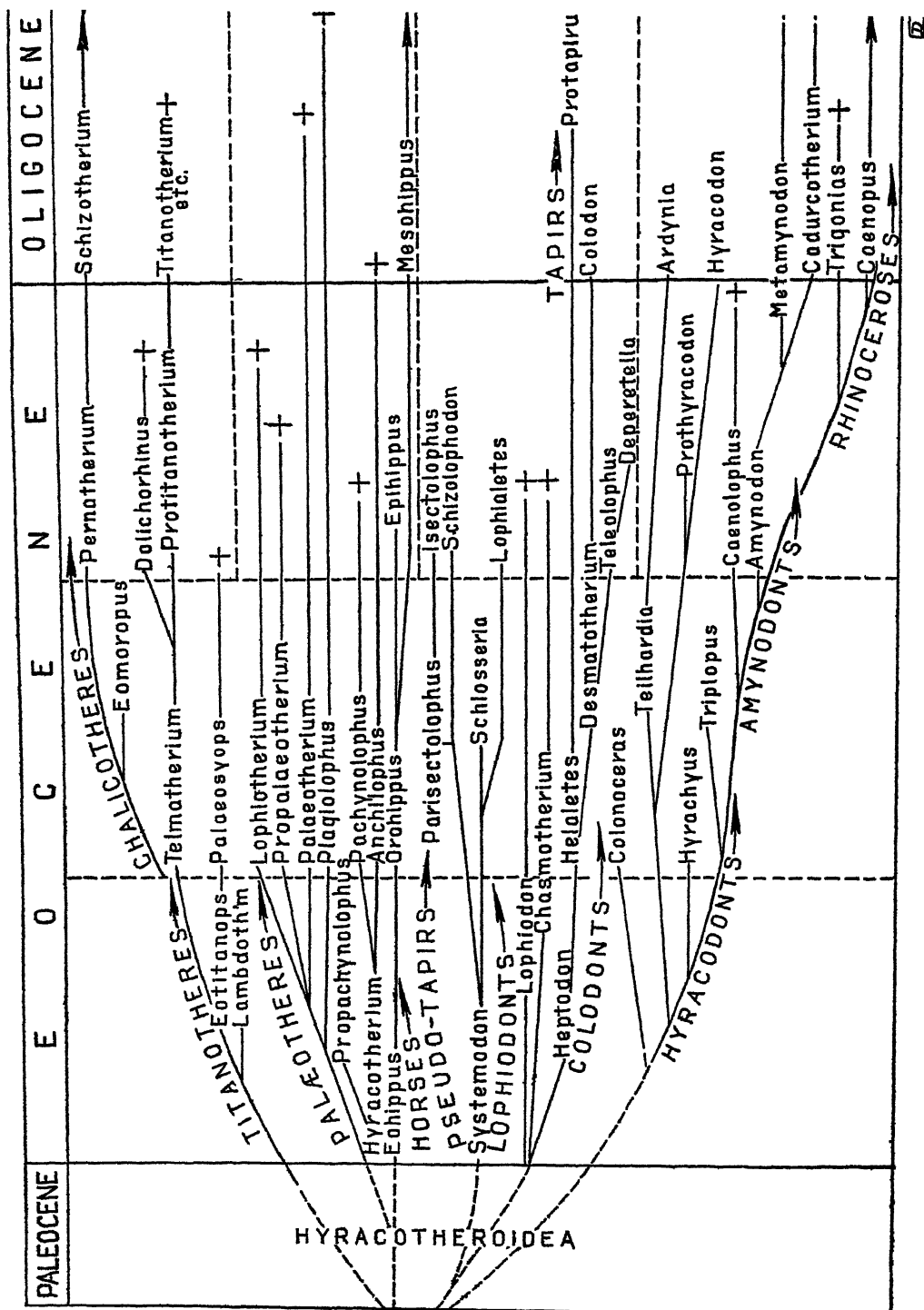


FIG. 26 DIVERGENT EVOLUTION OF THE PERISSODACTYLS IN THE OLDER TERTIARY

† The primitive group of hyracotheroids branches out during the Eocene into many phyla; separable in the Oligocene into four distinct groups through extinction of intermediate and synthetic types. During the later Tertiary these four groups continue their divergent specialization. Three still survive in the horses, tapirs

the early horses, the Anchitheriine horses parallel the rhinoceroses (to some extent). Such parallelisms, of which numerous cases might be cited, sometimes succeed and displace the older specialized adaptation. In other cases (including the three cited) they fail, and become extinct. The explanation of such success or failure is to be found in the effectiveness of the type as an animal mechanism, in its physical environment encouraging or forbidding the expansion and survival of the adaptive type, and its biotic environment providing or excluding competitive types in the region.

It is not possible within the limits of this essay to discuss even in outline the interpretation of the various specializations from the primitive Perissodactyl stock; but in the next section I will attempt to outline the probable interpretation of the evolution of the Equid phylum.

MEANING OF THE CHANGE IN FEET AND TEETH. PROGRESSIVE ADAPTATION TO CHANGING ENVIRONMENT

In attempting to understand the causes of the progressive development of the Equidæ as preserved in the geologic record, we must first look to the physical changes in the region they inhabited. At the beginning of the Eocene the Western Plains region was very different from what it is today. It had but recently emerged from the sea, and was still much nearer sea level than now. The climate was milder and the rainfall much greater than now, so far as one can judge from the flora; and it was rather a region of forest and glade than of broad open plains. The environment was that of sub-tropical forested regions, and it is in such regions that one may find today the analogues as well as the nearest relatives of the Eocene mammals. *Eobippus* may be compared with the pudu of Central

America and the tragulines of the Old World. It was probably a forest dweller, browsing on leaves and succulent herbage, the flexible four-toed foot adapted to the irregularities of the woods, to quick shifts and dodging behind covert, but not to speed over a uniform open surface.

During the Tertiary period there was a progressive rise of the great interior plains and cordilleran region, and change of climate. The rainfall became less, the tropical rain-forests retreated and the open glades expanded into broad grassy plains. Some of the animals, like the tapirs, retreated with the forests. Others, like the horses, adapted themselves to the new conditions. In great part the Evolution of the Horse is the record of this progressive adaptation.

The drier, harder grasses of the plains demanded more thorough trituration in order to make their food-values available. The change in the teeth is chiefly directed to the development of an efficient grinding apparatus for this purpose. This is secured, first by conversion of the premolars into molariform teeth, thus doubling the grinding surface, second through conversion of low, more or less rounded cusps into sharp crests and crescents, thus providing parallel shearing edges of enamel in the worn teeth as the lower jar sweeps across the surface of the upper in grinding the food. Next comes the elongation or heightening of the crowns of the teeth to prolong the life of this grinding apparatus. But with the elongation of this complex pattern of dentition it develops a weakness in the lack of support for the enamel, and a tendency to flake off, block the valleys and interfere with efficient grinding. This is obviated in Equidæ by development of cement, a softer material analogous to the dentine that is exposed inside the enamel, but deposited on the outside before the tooth cuts the gum. In the

THE EVOLUTION OF THE HORSE.

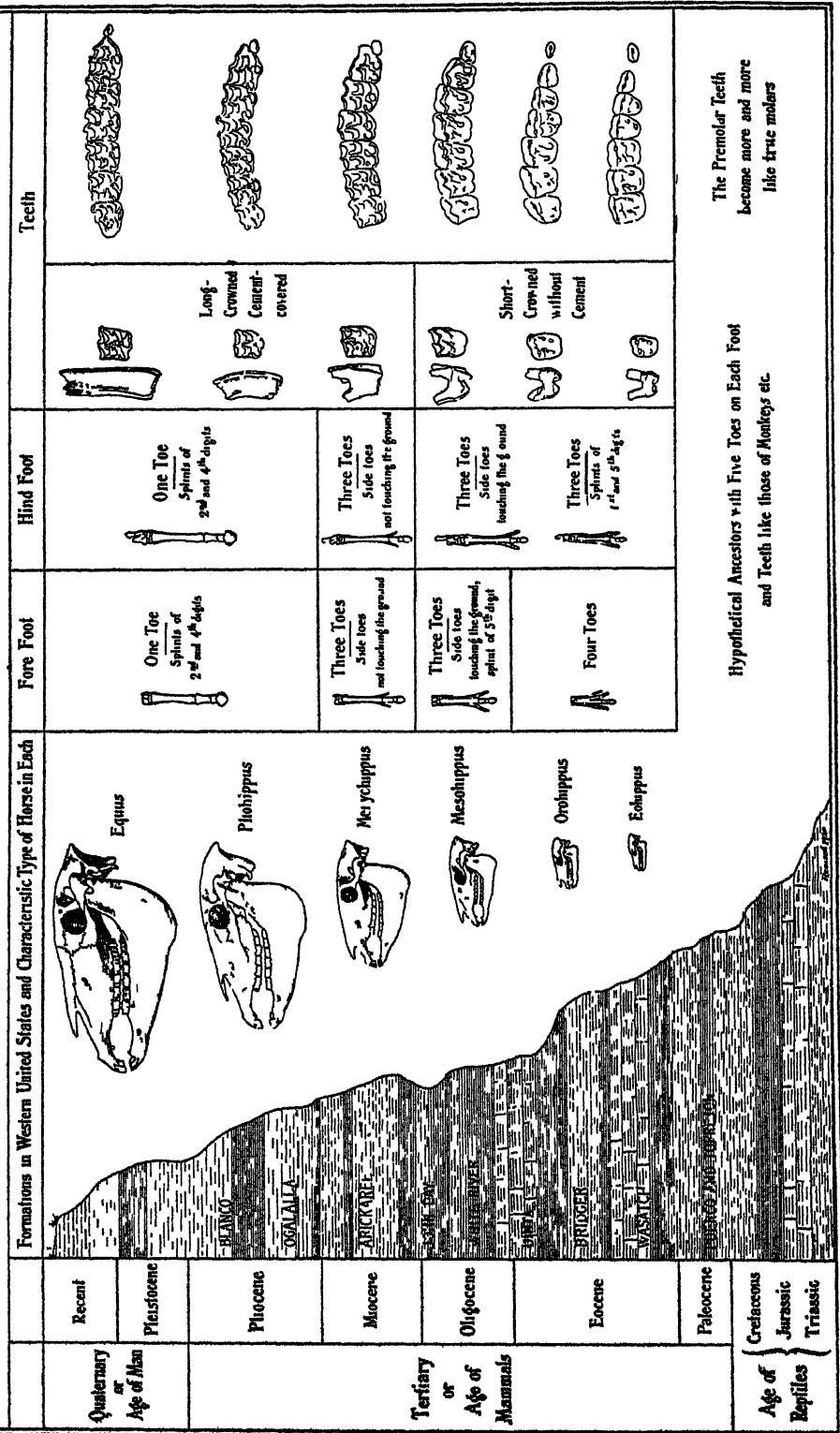


FIG. 27

modern horse the cement is deposited from fluids secreted by special glands (probably evolved during the later Tertiary from the salivary glands?). The development of cement, initiated in *Parahippus*, made possible a progressive elongation of the crown into a square prism which is pushed up from beneath as it wears off on the grinding surface, and might become in the further course of evolution rootless and continuous in its growth until the animal dies. This has occurred with various rodents; in the horse, however, the root of the tooth forms, and its growth ceases at about six years, after which it pushes upward in the jaw until it is completely worn down, when the animal can no longer chew his food and dies of malnutrition.

The change in limbs and feet is no less striking, and is equally explained as an adaptation to the progressively dry climate and open plains environment. Speed, especially long-distance speed, becomes essential to a defenseless herbivore living in open country. The plains surface is smooth and hard, and there is no need for flexible adaptable joints, or for side toes to adjust the step to an irregular surface. A long limb will cover more ground at each step, but if the proportions remain the same the step will be slower, as the normal swing of an animal's step is essentially a pendulum-swing. If the centre of gravity is shifted towards the upper part of the limb by lengthening its lower segments while shifting the muscles more into the upper part of the leg and moving the lower segments by long tendons, the length of step will be increased without decreasing the speed of its swing. Moreover, the reduction of the lateral digits and concentrating the step on a central digit will add to the speed by substituting a clean, quick drive from a tight-jointed, rigid hoof, for the soft,

yielding push of the five-toed foot. These changes put a heavier strain on joints and ligaments, and these must be strengthened, the movements of the segments concentrated on the lines of locomotion at the expense of flexibility, by extending the fore-and-aft movements but limiting the lateral movements. Hence the deepening of the pulley of the astragalus, the shifting of wrist and ankle bones so that the inner and outer ones acquire a footing on the cannon bone, development of a keel at the end of the cannon bone, and a whole series of minor changes that can easily be seen to serve the same general purpose.

At the same time the tibia and fibula of the hind leg, the ulna and radius of the fore leg, originally two separate bones permitting considerable torsion at this joint, become more closely united, consolidate, and the shafts of the ulna and fibula become vestigial, the torsion of the joint wholly lost.

These limb changes involve changes in the proportions of the body and head. The neck and head must be lengthened out in order to enable the animal to graze. The barrel becomes shorter, deeper, less flexible, conformant with the limitation of the limb and foot movements, and again acquiring strength and speed at expense of flexibility.

A second series of changes in proportions and structure is related to increase in size. The advantage of increased size to an animal in competing with rivals or keeping off enemies is obvious enough, and up to a certain limit it results in increased speed. The disadvantage is based upon the well known engineering fact that the relative strength of a structure decreases with its size, as the strength is proportioned to the cross-section, but the weight to the mass. This is also true of the muscles; their strength is proportioned to

their cross-section, their weight to their bulk. Hence, with increase in size the bulk of the animal increases as the cube of the linear dimensions, while the strength of the bones and muscles increases as the square of the linear dimensions. This must be offset by relative increase in the robustness of bones and massiveness of muscles. But the food requirements for the more massive muscles are also relatively increased, while the area covered in grazing increases with the larger animal only as the square of the linear dimensions. It results that larger animals need a good deal more food in proportion to their size, and, as a matter of observation, large animals spend a great portion of their time in feeding, while smaller animals can satisfy their relatively smaller food requirements in a small proportion of their time. This sets a limit to the size of an animal as a practical working mechanism, a limit that varies with the nature and abundance of the food and the perfection of the mechanism, and is affected by various other factors. (The more rapid metabolism necessary to maintain a constant high body temperature in a smaller animal affects the food requirements in an opposite sense to the above; but it is of less relative importance in mammals of the size here considered.)

The maximum of speed in a quadruped is reached at an earlier stage. Up to that stage the increase in size, although it involves a relative decrease in speed, enables the animal to cover more space within a limit of time. Beyond it, the greater massiveness necessary reduces the absolute speed. The swiftest living animals are of the size of the gazelles and smaller antelopes, and the three-toed horses of the later Miocene were probably swifter than their modern descendants. The larger animal, however, is more able to defend himself against enemies, and

as long as his food is sufficiently abundant natural selection will develop races considerably beyond the point of maximum speed. This has happened with the horses, the larger antelopes and cattle and various other races. With all large animals, however, an adequate food supply is a relatively important factor in their survival, specialized habits become essential in order to secure sufficient food, and large animals are hence more liable to extinction through change of environment, and for other reasons which it would take too long to discuss.

We observe in the evolution of the horse a progressive elongation of the lower legs and feet, with disappearance of the side toes, and the various minor mechanical adjustments necessary to secure high speed. This reaches a maximum in the Miocene and Pliocene horses, and, in the Pleistocene and modern horses, especially the larger species have relatively shorter and more robust leg and foot bones. They have passed the speed maximum, and probably have reached the size maximum for that particular adaptation and environment. Modern horses are no larger than those of the Lower Pleistocene.

Many other changes in the construction and proportions of all parts of the skeleton have taken place *pari passu* with the changes cited. Most of them are obviously explained on the mechanical and adaptive principles outlined. The increase in brain capacity is a line of progress paralleled by most other successful races of mammals. It involves probably a great diversity of specialized adaptations of intelligence to the habits of the animal, but its real meaning can hardly be understood in the present state of our knowledge. The horse has undoubtedly developed a marvellous place-memory, and the special development of its brain has presumably centred largely on this

feature, conditioning the special pattern seen in the progressive complication of the convolutions.

The development and final degeneration of the facial pockets or preorbital fossæ is also an obscure point. Gregory (1920) has shown that these probably lodged diverticula of the nasal passages, but their function and usefulness is not known.

SIMILAR CHANGES IN OTHER ANIMAL GROUPS.

PARALLEL ADAPTATION IN OTHER MAMMALS

If our explanation of the progressive changes in the Equidæ phylum is correct, we should find other animals doing the same thing. That is to say, other races of similar habits, subject to the same changes of environment, should parallel the Equidæ more or less closely. They should develop a superficial similarity, with underlying differences of construction that betray the different origin. Such we find to be the case. Among the great group of Artiodactyls (pigs, hippopotami, deer, antelopes, cattle, etc.) all the ruminants are seen in their geologic record losing the side toes, concentrating the step upon a central pair which become co-ossified into a "cannon bone" as in the horses, only with two hoofs instead of a single broad hoof. The teeth also become elongated with four crescents as in the horse, and in the cattle and some antelopes a large, high inner pillar on the molars and a heavy investment of cement make the molars singularly like those of horses. The premolar teeth, however, do not become like the molars; this deficiency in numbers of the grinders is offset by the habit of ruminating or chewing the cud.

In South America, in absence of true horses, another group of hoofed animals, the Litopterna, now wholly extinct, evolved a race which paralleled the horses in a very interesting way. They de-

veloped three-toed and one-toed types which resemble the true three-toed and one-toed horses superficially, but in details of construction are seen to be even more different than Tapir or Rhinoceros. Their teeth likewise resemble the teeth of the earlier three-toed horses, and likewise differ more widely in the underlying construction than do the diverse families of Perissodactyls of the north. (Yet these resemblances have been close enough to deceive able palæontologists in the past, when the evidence was more scanty than it is today.) When the true horses invaded South America in the Pliocene, these pseudo-horses became extinct. They had carried the specialization of the feet a stage further even than the modern horse, in one genus at least: *Thoatherium* has the side toes reduced to small nodules of bone; but this animal is quite small, about the size of a gazelle. Contemporary with it was a larger form, *Diadiaphorus*, with side toes reduced about as in the contemporary *Merychippus*. The teeth, however, are not beyond the stage reached in *Miohippus* of the Upper Oligocene.

THE BEARING OF THIS EVIDENCE ON EVOLUTION

In the preceding pages has been outlined a summary of the material facts of evidence in the case. The fossils, found in a certain sequence of geological formations, are the actual remains of animals that lived when that succession of formations was being deposited. They are a direct record of the geological history of the equine family, that is, of the animals anatomically related to the existing horses. There is no question about the succession of the formations; they have been traced across country, one overlying or overlapping another in such fashion that the sequence is certain. There is no

question that the various stages are found in their appropriate position in the geologic succession as recited above, and are found only within those limits as specified. This is proved by many thousands of specimens of the better known stages and by hundreds of nearly all the rarer stages, which have been found by various collecting parties during the last eighty years, especially during the last two decades, and are preserved in various museums, each with exact record of formation and locality in which it was found. Collectors have been keenly on the lookout for exceptions, for such exceptions would be of extraordinary interest to science; but they have not been found. Even certain *apparent* exceptions when more carefully studied have been found not to be real exceptions.

Broadly speaking, the evolution of the horse in the sense of a regular progression by gradual stages from small primitive four-toed ancestors to the large, highly specialized, one-toed horse, appears not as a theory but a fact of record. It is equally a fact of record that the tapir and rhinoceros are derived from the same primitive stock through a similar series of progressive stages. Widely different in appearance and habits today, they have diverged from a common ancestral stock.

If, therefore, we turn to the record of geologic history to answer the question whether as a matter of fact the diverse types of existing animals did evolve from common primitive stocks, or whether the various races have remained unchanged since they were created, the answer is perfectly definite and categorical. Whenever the evidence is sufficient, as it is in this instance, it proves the theory to be a fact of record. When the evidence is insufficient for proof, it fits in with the evolution theory, so far as it goes. It is in comparatively few instances out of the

millions of existing species that the categorical proof of their evolution is at hand. This will always be true, although the number of proofs and the completeness of the evidence grows year by year.

It is asserted by some opponents of evolution that "the evidence is all circumstantial." Probably what they mean is the anatomical evidence—which, moreover, they totally misconceive in saying that it is "a matter of resemblances." The fossil evidence, however, is not circumstantial; it is the direct testimony of the record itself, far better than "eye-witness testimony," for eye-witnesses may easily be mistaken, and often are, and there is no way to discover and correct their mistakes save the imperfect and uncertain methods of collation and cross-examination. As for the evidence of comparative anatomy, while it is indirect, and may be compared to circumstantial evidence, its weight lies not at all in "resemblances" but in identity of structural plan underlying a wide *diversity* of appearance and habits. We regard horse and man as related, not because they resemble each other, for they are utterly diverse in appearance, but because in spite of this diversity the anatomist finds that their underlying structure is fundamentally the same.

The causes and methods of the evolutionary process are matters of theory. The fossil record throws much light upon some of the problems involved; others are wholly outside of its field. From detailed study of abundant material within a limited portion of the record, the range of individual variation of the animals in a certain area can be followed through the considerable period represented by a fossiliferous formation or succession of formations. Whether or to what extent these lie in genetic descent is a matter of relative probability, not of direct evidence.

Migration, the continuous shifting of range and species, invading new regions and abandoning old habitats, must always play a part, probably a dominant part, in the making of such a record. The gaps or apparently sudden jumps in a well documented phylogeny often ascribed to "mutation" are, in most cases, due rather to migration. This much can be said, that the more complete the record, the more abundant the material, and the nearer we are, judging from the available evidence, to the probable centre of evolution and dispersal of any race of animals, the more continuous does the succession become, the more it appears to evolve through a succession of minute changes which lie within the limits of ordinary individual variation.

For the facts as to the nature and kinds of individual variations and the laws of their inheritance or non-inheritance, the palæontologist must turn to the geneticist. But it is apparent that the large and obvious "mutations" which the geneticists select for "experimental evolution" have not played any part in natural evolution as observed by palæontologists. Probably the same laws of inheritance which they have deduced from the study of these large "mutations" apply equally to the minute and very frequent heritable variations whose existence in ourselves and familiar animals has always been a matter of common knowledge. It is equally true of fossil animals, that no two are exactly alike, equally probable *a priori* that the variations are partly heritable, partly non-heritable, and that heritable variations are acted upon by natural selection. Some geneticists have shown us why such variations cannot accumulate into diversity of species and genera; but the palæontological record shows that they do, and the fallacy that lies behind the geneticists' argument is not difficult to discover.

This fallacy turns partly upon a feature of nature as against artificial selection that it is not easy for a zoölogist to appreciate, namely, the exceeding slowness of evolutionary changes in nature, and the vast length of geologic time. The Pleistocene period covers, according to recent estimates, more than a million years, more, that is to say, than a hundred thousand generations. Yet the amount of change in the horse phylum during that time is measured by the difference between one species and another. Artificial breeding produces in a hundred generations corresponding or greater changes in certain parts, but then comes against an apparent barrier to further change because the heritable variations necessary to accumulate further changes and co-ordinate them with other parts of the mechanism are not potentially available in the limited numbers of the stocks used for breeding. But in nature the stocks are not so limited; they consist of many millions of individuals scattered over one or several continents, and intermingled and crossed through the shifting of range and migration over a period a thousand times as long. If we assume that new heritable variations appear from time to time in the heredity of each herd—and common knowledge of the heredity of our own species makes this appear rather as observation than assumption—the number of potential variations available for breeding will be quite limited in dealing with a single herd over a few generations, but practically unlimited in natural selection through geologic time.

Now any wide departure from the normal in an individual is not advantageous because it interferes with the effectiveness of the animal as a working mechanism, and cannot be adjusted by numerous other changes of corresponding amount necessary in order to make the machinery work effectively.

To amputate the side toes from a dog would cripple it, not help it, because the central pair are not strengthened, the muscles are not adjusted to the new conditions, a hundred other correlated changes are not present. On the other hand, a slight change, a little elongation of the limbs or feet can be, and is normally, adjusted through the growth of the animal. These adjustments are not inherited; they cannot accumulate. So that while the heritable difference can accumulate, it soon reaches a point where the necessary co-ordinations are too great to be made through adjustments during the growth of the individual, the further evolution of the character ceases to be of advantage because it becomes a mal-adjusted mechanism, and until heritable variations can be introduced into the heredity to replace these non-heritable adjustments, no further progress can be made. Time and intercrossing will finally overcome this lack; it is a brake on evolutionary progress, not a barrier, but it may explain why the record shows evolution to progress with such extreme slowness. The palæontologist has indeed a different

scale; he often speaks of rapid evolution and even of "explosions" of phyla. But an explosion which took at the least many thousands of centuries to explode would not seem to the lay mind to be so very sudden; and in fact I doubt whether there is any real evidence of more rapid evolution than the change from *Eohippus* to *Equus*, and that, 'if the radium calculations are correct, took some fifty million years. It covers ten intermediate generic stages, and, if we assume that valid species are one-tenth as far apart as valid genera, we would figure that it took on the average five hundred thousand years to change from one species to the next in descent. The palæontologist, accustomed to his astronomical time-scale, may speak of the extremely rapid evolution of Tertiary mammals in contrast to the (relative) fixity of the turtles and crocodiles—but what he means by "extremely rapid" is a barely perceptible mutation in half a million years. (Barely distinguishable, that is to say, from mere individual variation. The quotation is from Osborn's recent address "The Origin of the Species as Revealed by Vertebrate Palaeontology.")

LIST OF LITERATURE

- AMBROGINO, FL. 1889. Mamíferos Fósiles de la Republica Argentina. Act. Acad. Nac. Cienc. Cordoba, vol. VI, pp. i-xxxii, 1-1027, pll. i-xcvi. [Pp. 502-523 review the Argentine Pleistocene Equidæ.]
- AMBROGINO, FL. 1891. Observaciones críticas sobre los caballos fósiles de la Republica Argentina. Rev. Arg. Hist. Nat., t. I, pp. 4-17, 65-88.
- AMBROGINO, FL. 1904. Recherches de morphologie phylogénétique. Anal. Mus. Nac. Buenos Aires, t. IX, pp. 1-541. [An extended argument for the views held by the author concerning the phylogeny of various mammals, including Equidæ.]
- AMBROGINO, FL. 1907. Sobre dos esqueletos de mamíferos fósiles . . . en el Museo Nacional. Anal. Mus. Nac. Buenos Aires, t. xvi, pp. 35-43. [Mounted skeleton of *Hippidium*.]
- ANDREWS, C. W. 1902. A Pliocene vertebrate fauna from the Wadi Natrum, Egypt. Geol. Mag. N. S., vol. ix, pp. 433-439. [*Hippurion* from Egypt.]
- ANTONIUS, O. 1919. Untersuchungen über den phylogenetischen Zusammenhang zwischen *Hippurion* und *Equus*. Zeitschr. f. induc. Abstam. u. Vererb. Bd. xx, s. 273-295. [Maintains that *Hippurion* cannot be excluded from the ancestry of *Equus*.]
- BARBOUR, E. H. 1914. A new fossil horse *Hypophippus matthewi*. Rep. Neb. Geol. Sur., vol. iv, pp. 169-173, pll. 1-11.
- BOAS, J. E. V. 1881. Om en Fossil Zebra-form fra Braziiliens Campos . . . Vidensk. Selsk. Skr., 6 Räk. nat.-math. Afd. 1str. Bd. V, s. 306-330. [*Equus* and *Hippidium*; ideas as to phylogeny.]

- BORISSIAK, A. 1914. Mammifères fossiles de Sébastopol. Mém. Comité Géol., N. S., livr. 87, Egger et Cie. St. Petersburg.
- BOULE, MARCELLIN. 1899. Observations sur quelques Equidés fossiles. Bull. Soc. Geol. France (3) vol. xxvii, p. 531-542. [Confirms Mmc. Pavlow's view that *Hipparion* is not a direct ancestor of *Equus*.]
- BOULE, MARCELLIN. 1910. Les Grottes de Grimaldi. I Geologie et Paléontologie, fasc. iii. Imprimerie de Monaco. [Fossil *Equus* from Grimaldi caves and affinities of species of *Equus*, pp. 175-192, pll. xvii-xix.]
- BOULE, MARCELLIN. 1920. Mammifères fossiles de Tarija Mission Scientifique Crequi-Montfort. (Report on collections, 255 pp. text, 27 pll. and 65 text figures), Paris, France. [Equidæ of Tarija and discussion of affinities of South American Pleistocene Equidæ.]
- BRADLEY, O. C. 1904. On the trapezium of the horse. Proc. R. phys. Soc. Edinb., vol. xvi, pp. 9-18. [Trapezium present in about fifty per cent of skeletons examined.]
- BRANCO, W. 1883. Ueber eine Fossile Säugethier-Fauna von Punin bei Riobamba in Ecuador. Palæont. Abh., Dames u. Kayser, Bd. I, Heft 2. [*Equus andium*, description of skull and skeleton and discussion of phylogeny of Equidæ, pp. 20-110, pll. vii-xvii.]
- BURMEISTER, H. 1875. Los caballos fósiles de la pampa Argentina. Published for the Provincial Government of Buenos Aires Exhibit at the Centennial Exhibition, Philadelphia, 1876. [Descriptions and illustrations of *Hippidium* and other extinct Argentine horses.]
- CARDOSO, A. 1912-3. Antigüedad del caballo en el Plata. Anal. Mus. Nac. Buenos Aires, t. xv, p. 371-439; t. xxiv, p. 445-460.
- CHUBB, S. H. 1912. Notes on the trapezium in the Equidæ. Bull. Amer. Mus. Nat. Hist., vol. xxxi, pp. 113-115. [Occurrence in about one out of eight domestic horse skeletons.]
- CHUBB, S. H. 1921. The Horse Under Domestication. In Evolution of the Horse. Amer. Mus. Nat. Hist. Guide Leaflet Series, No. 36.
- COPE, E. D. 1877. Extinct Vertebrata obtained in New Mexico by Parties of the Expedition of 1874. Report. Geog. Sur. W. of 100th Merid., vol. iv, Palæontology, Part II. [Descriptions of Lower Eocene and Upper Miocene Equidæ from New Mexico, pp. 252-268, 321-323, pll. lxxv, lxxvi, lxxv.]
- COPE, E. D. 1882. Contributions to the history of the vertebrata of the Lower Eocene of Wyoming and New Mexico. Proc. Amer. Phil. Soc., 1881-2, pp. 139-197. [*Hyracotherium*, etc., first descriptions.]
- COPE, E. D. 1878. On some of the characters of the Miocene fauna of Oregon. Proc. Amer. Phil. Soc., Nov. 15.
- COPE, E. D. 1884. The extinct Mammalia of the Valley of Mexico. Proc. Amer. Phil. Soc., vol. xxii, pp. 10-11.
- COPE, E. D. 1885. Tertiary Vertebrata. Report U. S. Geol. Sur., vol. III, Book i. [Description and figures of skeleton of *Hyracotherium* (*Eobippus*), pp. 624-652, pll. lxix a, lxix b, lxix c.]
- COPE, E. D. 1886. On two new species of three-toed horses from the Upper Miocene. . . . Proc. Amer. Phil. Soc., vol. xxiii, pp. 357-371.
- COPE, E. D. 1887. The Perissodactyla. Amer. Nat., vol. xxi, p. 1072. [Review of the evolution and American record.]
- COPE, E. D. 1889. A Review of the North American species of *Hippotherium*. Proc. Amer. Phil. Soc., vol. xxvi, pp. 429-458. [*Hipparion*.]
- COPE, E. D. 1891. On the skull of *Equus excelsus* Leidy. . . . Amer. Nat., pp. 912-913.
- COPE, E. D. 1893. Preliminary Report on the Vertebrate Palæontology of the Llano Estacado. Geol. Surv. Texas, Fourth Ann. Report, pp. 1-87 and pll. i-xxiii of separate. [Description of Miocene, Pliocene and Pleistocene species and revision of *Protobippus*.]
- COPE, E. D. AND W. D. MATTHEW. 1915. Tertiary Mammalia and Permian Vertebrata. Amer. Mus. Nat. Hist. Mon. Ser. No. 2. [Plates prepared under direction of Professor Cope for the unpublished second book of vol. iii of Rep. U. S. G. S. Plate descriptions by W. D. Matthew. Seven plates, Nos. 145-151 illustrate Miocene Equidæ.]
- DEPÉRET, CH. 1892. La Faune de mammifères Miocènes de la Grive St. Alban. Arch. Mus. d'Hist. Nat. Lyon, t. v.
- DEPÉRET, CH. 1917. Monographie de la Faune de Mammifères Fossiles du Ludien d'Euzet-les-Bains (Gard). Ann. Univ. Lyon, N. S. (1), fasc. 40, pp. i-viii, 1-288, pll. i-xxv. [*Aschilophus*, *Lophiotherium*, pp. 62-91, pll. xii-xv; phylogeny pp. 264-269.]
- DOUGLASS, E. 1903. New vertebrates from the Montana Tertiary. Ann. Carn. Mus., vol. ii, pp. 145-200.
- DOUGLASS, E. 1908. Fossil horses from North Dakota and Montana. Ann. Carn. Mus., vol. iii, pp. 267-277, 4 plates.
- DURST, J. U. 1908. Animal Remains from the Excavations at Anau. . . . Carnegie Institution Publ. No. 73, chaps. xvi-xix, pll. 71-91.

- [Relations of prehistoric races at Anau, Turkestan, to modern domestic horse.]
- EWART, J. C. 1894. The development of the skeleton of the limbs of the horse with observations on polydactyly. *Jour. Anat. Phys.*, vol. xxviii, pp. 236-256, 342-369.
- EWART, J. C. 1904. The multiple origin of horses and ponies. *Trans. Highland Agric. Ass., Scotland*, pp. 1-39.
- EWART, J. C. 1907. The derivation of the modern horse. *Quart. Review*, vol. 206, pp. 547-574.
- EWART, J. C. 1907. On skulls of horses from the Roman fort at Newstead. *Trans. Roy. Soc. Edinb.*, vol. xlv, pt. iii, pp. 555-587.
- EWART, J. C. 1909. The possible ancestors of the horse living under domestication. *Science*, vol. xxx, pp. 219-223.
- FALCONER, H. 1868. *Palæontological Memoirs and Notes*. Compiled and Edited by Chas. Murchison. London, 1868. [Vol. 1, Siwalik Equidæ, *Equus* and *Hipparion*.]
- FARR, M. S. 1896. Notes on the osteology of the White River horses. *Proc. Amer. Phil. Soc.*, 1896, p. 147. [Restoration of *Mesobippus* skeleton.]
- FLOWER, W. H. 1885. *An Introduction to the Osteology of the Mammalia*. 3rd Ed., London. [Concise and clear summaries of the principal features of skull and skeleton in modern mammals. Teeth not included.]
- FLOWER, W. H. 1891. *The Horse*. London. Kegan, Paul, Trubner Co.
- FRICK, CHILDS. 1921. Extinct vertebrate fauna of the Badlands of Bautista Creek and San Timoteo Canon, Southern California. *Univ. Cal. Publ., Bull. Dept. Geol.*, vol. xii, pp. 277-424, pll. xliii-1, 165 text figs.
- GAUDRY, A. 1862. *Animaux Fossiles et Géologie de l'Attique*. Paris. 4to. [Description of *Hipparion* from Pikermi.]
- GAUDRY, A. 1866. Sur les Hipparions. *Bull. Soc. Geol. France*, t. xxii, pp. 21-24. [Frequent occurrence of vestigial fifth metacarpal and trapezium.]
- GAUDRY, A. 1873. *Animaux Fossiles du Mont Leberon (Vaucluse)*. 4to. Paris. [*Hipparion*, pp. 325-42, pll. v-vii.]
- GERVAIS, P. 1859. *Zoologie et Paléontologie Français*. Deuxième Ed. Paris. [Livre I, Chap. 1, Equidæ.]
- GERVAIS, P. 1867-9. *Zoologie et Paléontologie Générales*. 4to. Paris. [*Hipparion*, pp. 147-170.]
- GERVAIS, P. 1885. *Recherches sur les Mammifères Fossiles de l'Amérique Méridionale*. 4to. Paris.
- GIDLEY, J. W. 1901. Tooth characters and revision of the North American species of the genus *Equus*. *Bull. Amer. Mus. Nat. Hist.*, vol. xiv, pp. 91-142, pll. viii-xxi, 27 text figures. [Revision of species, based chiefly upon studies of *Equus scottii* skeletons and of large series of jaws and bones from the Hay Springs quarry.]
- GIDLEY, J. W. 1903. A new three-toed horse. *Bull. Amer. Mus. Nat. Hist.*, vol. xix, pp. 465-476. [First description of *Neohipparion whitneyi* skeleton.]
- GIDLEY, J. W. 1904. Proper generic names of Miocene horses. *Bull. Amer. Mus. Nat. Hist.*, vol. xx, pp. 191-194.
- GIDLEY, J. W. 1906 [with W. D. Matthew]. New or little known mammals from the Miocene of South Dakota. *Bull. Amer. Mus. Nat. Hist.*, vol. xxii, pp. 135-153, 19 text figures. [Description of topotype material of several of the classic species of Leidy.]
- GIDLEY, J. W. 1907. Revision of the Miocene and Pliocene Equidæ of North America. *Bull. Amer. Mus. Nat. Hist.*, vol. xxiii, pp. 865-934. [Revision of species of later Miocene three-toed horses, with observations on the phylogeny.]
- GILMORE, C. W. 1908. Smithsonian Exploration in Alaska in 1907 in Search of Pleistocene Fossil Vertebrates. Second Expedition. *Smiths. Misc. Coll.*, vol. li, pp. 3-38. [*Equus* in Alaska.]
- GRANGER, WALTER. 1908. Revision of the American Eocene horses. *Bull. Amer. Mus. Nat. Hist.*, vol. xxiv, pp. 221-264, pll. xv-xviii, 5 text figures.
- HAY, O. P. 1913. Notes on some fossil horses with descriptions of four new species. *Proc. U. S. Nat. Mus.*, vol. xlv, pp. 569-594, pll. lxix-lxxiii. [Descriptions of *Equus leidy*, *litoralis*, *niobrarensis* and *laurentius* (the last is based upon a recent skull mistakenly supposed by the author to be of Pleistocene age).]
- HAY, O. P. 1914. The Pleistocene mammals of Iowa. *Iowa Geol. Sur.*, vol. xxiii, pp. 3-499, pll. i-lxxv. [Pleistocene Equidæ and *Neohipparion*, pp. 143-209, pll. viii-xviii.]
- HAY, O. P. 1915. Contributions to the knowledge of the mammals of the Pleistocene of North America. *Proc. U. S. Nat. Mus.*, vol. xlviii, pp. 515-575, pll. xxx-xxxvii. [Descriptions of *Equus hatcheri* and *francisi*, discussion of species from European Pleistocene and origin of domesticated horse.]
- HAY, O. P. 1917. Description of a new species of extinct horse *Equus lambei*, etc. *Proc. U. S. Nat. Mus.*, vol. liii, pp. 435-443, pll. lvi-lviii. [Skull of a fossil horse from Yukon territory.]

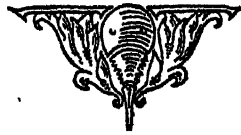
- HAY, O. P. 1923. The Pleistocene of North America and its Vertebrated Animals from the States East of the Mississippi River. . . . Carnegie Institution Publ., No. 322. [Equidæ, pp. 183-202.]
- HAY, O. P. 1924. The Pleistocene of the Middle Region of North America and its Vertebrated Animals. Carnegie Institution Publ., No. 322 A. [Equidæ, pp. 122-154.]
- HENSEL, R. 1860. Ueber *Hipparion mediterraneum*. Abh. Akad. Wiss. Berlin. [Description of the three-toed horse of Southern Europe.]
- HERNANDEZ-PACHECO, E. 1915. Geologia y Paleontologia del Mioceno de Palencia. Com. Invest. Pal. y Prehist., Mem. No. 5, Mus. Nac. Cienc. Nat. Madrid. [*Anchitherium* in Spain, pp. 102-112, pl. xlii-xlv.]
- HERNANDEZ-PACHECO, E. 1921. La Llanura Manchega y sus Mamíferos Fósiles. Com. Invest. Pal. y Prehist., Mem. No. 28, Mus. Nac. Cienc. Nat. Madrid. [*Hipparion* in Spain.]
- HUXLEY, T. H. 1870. Anniversary Address of the President of the Geological Society, London. In Collected Memoirs, vol. III, originally published in Q. J. G. S., vol. xxvi. [Evolution of horse traced through Old World genera, pp. 533-536.]
- HUXLEY, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly to the Mammalia. Proc. Zool. Soc. Lond., 1880, No. XI, iii, pp. 649-661.
- KOKEN E. 1885. Ueber Fossile Sacugethiere aus China. Pal. Abh. Dames u. Kayser, Bd. III. [*Hipparion* and *Equus* from China.]
- KOWALEVSKY, W. 1873. Sur l'*Anchitherium aurelianense* Cuv., et sur l'Histoire Paléontologique des Chevaux. Mem. Imp. Acad. Sci. St. Petersburg, t. xx, No. 5. [Classic memoir on the evolution of the horse, traced through *Hipparion*, *Anchitherium* and the palæotheres. See Huxley, 1870, for preliminary sketch.]
- LEIDY, JOSEPH. 1869 Extinct mammalian fauna of Dakota and Nebraska. Jour. Acad. Nat. Sci. Phila., vol. vii. [Numerous American species of three-toed horses described in this volume. Bibliography of previous literature.]
- LEIDY, JOSEPH. 1896. [F. A. Lucas, editor.] Fossil vertebrates of the Alachua Clays, Florida. Trans. Wagn. Inst. Sci., vol. iv.
- LOOMIS, F. B. 1908. A new horse from the Lower Miocene. Amer. Jour. Sci., vol. xxvi, pp. 163-165, 1 figure. [Description of *Parahippus tyleri*.]
- LUCAS, F. A. 1900. The ancestry of the horse. McClure's Magazine.
- LUCAS, F. A. 1901. Animals of the Past. McClure, Phillips and Co., New York.
- LULL, R. S. 1907. The evolution of the horse family. Amer. Jour. Sci., vol. xxiii [Guide to the collections of fossil horses in the Peabody Museum, Yale University.]
- LULL, R. S. 1913. The Yale collection of fossil horses. Collections of Yale University, No. 1.
- LYDEKKER, R. 1882. Indian Tertiary and post-Tertiary Vertebrata. Siwalik and Narbada Equidæ. Palæont. Indica, Ser. x, vol. ii, pp. 67-98. [Description of *Equus* and *Hipparion* remains from India.]
- LYDEKKER, R. 1884. Additional Siwalik Perissodactyla, etc. Palæont. Indica, Ser. x, vol. iii, pt. i. [*Hipparion*.]
- LYDEKKER, R. 1918. The Horse and Its Relatives. Macmillan, New York. [Semipopular account of the existing and extinct Equidæ; the latter based upon the author's researches upon Old World Tertiary Equidæ and upon Lull's Guide of 1907.]
- MAJOR, FORSYTH. 1877. Beit. zur Gesch. der Fossilen Pferde insbesondere Italicens.
- MARSH, O. C. 1871. Notice of some new fossil Mammals from the Tertiary formation. Amer. Jour. Sci. (3), vol. ii. [*Anchitherium gracile* (= *Epihippus*), first Eocene American Equine.]
- MARSH, O. C. 1872. Preliminary description of new Tertiary mammals, Part II. Amer. Jour. Sci. (3), vol. iv, pp. 202-224. [*Orohippus*.]
- MARSH, O. C. 1873. Notice of new Tertiary mammals. Amer. Jour. Sci. (3), vol. v, pp. 407-410. [*Orohippus*.]
- MARSH, O. C. 1874. Notice of new Equine mammals from the Tertiary formation. Amer. Jour. Sci. (3), vol. vii, pp. 247-258. [*Miohippus*, *Pliohippus*. First reconstruction of the ancestry of the horse from American fossils.]
- MARSH, O. C. 1875. Notice of new Tertiary mammals. Amer. Jour. Sci. (3), vol. ix, pp. 239-250. [*Mesohippus*.]
- MARSH, O. C. 1876. Notice of new Tertiary mammals. Amer. Jour. Sci. (3), vol. xii, pp. 401-404. [*Eohippus*.]
- MARSH, O. C. 1879. Polydactyle horses, recent and extinct. Amer. Jour. Sci. (3), vol. xvii, pp. 499-505. [American ancestry of the horse, with diagrams showing the evolutionary stages.]
- MATTHEW, W. D. 1903. Evolution of the Horse. Guide Leaflet No. 9, Amer. Mus. Jour., vol. iii, No. 1 (January). Second Edition, 1905.

- [Popular sketch of the Evolution of the Horse, with special reference to American Museum collections.]
- MATTHEW, W. D. 1908. Exhibit illustrating the evolution of the horse. Amer. Mus. Jour., vol. viii, pp. 117-122.
- MATTHEW, W. D. AND H. J. COOK. 1909. A Pliocene fauna from Western Nebraska. Bull. Amer. Mus. Nat., vol. xxvi, pp. 364-414. [Fragmentary remains of various later Tertiary Equidæ.]
- MATTHEW, W. D. 1910. Continuity of development. Popular Science Monthly; vol. lxxii, pp. 473-478. [Saltation *versus* continuous progression in phylogeny of fossil vertebrates. Effects of progressive migration and hybridism.]
- MATTHEW, W. D. 1912. The new four-toed horse skeleton. Amer. Mus. Jour., vol. xii, p. 186.
- MATTHEW, W. D. AND S. H. CHUBB. 1913. Evolution of the Horse Guide Leaflet No. 36, Amer. Mus. Nat. Hist. Part I, pp. 1-35, by Matthew, Evolution of the Horse in Nature. Part II, pp. 39-63, by Chubb, The Horse under Domestication. Republished 1921 with minor revision. [Popular sketch of the extinct and existing horses with special reference to the American Museum collections. Bibliography of thirty titles is appended.]
- MATTHEW, W. D. 1914. Origin of Argentine wild horses. Nature, Feb. 12, p. 661.
- MATTHEW, W. D. 1915. Climate and evolution. Ann. N. Y. Acad. Sci., vol. xxiv, pp. 171-318, 33 text figures. [Fossil record and geographical dispersal of Equidæ, pp. 234-237.]
- MATTHEW, W. D. 1915. Problems of American Geology. Chap. vii, The Tertiary sedimentary record and its problems. Yale University Press. [Record of Equidæ in western North America, pp. 451-456.]
- MATTHEW, W. D. 1916. The horse and his progenitors. Science Conspectus, vol. vi, pp. 1-15.
- MATTHEW, W. D. 1916. Methods of correlation by fossil vertebrates. Bull. Geol. Soc. Amer., vol. xxvii, pp. 515-524. [Equidæ taken as standard for correlation of American epicontinental Tertiary horizons.]
- MATTHEW, W. D. 1917. Absence of the pollen in Perissodactyla. Bull. Amer. Mus. Nat. Hist., vol. xxxvii, pp. 573-577.
- MATTHEW, W. D. 1920. Three-toed horses. Natural History, pp. 473-478.
- MATTHEW, W. D. 1924. Third contribution to the Snake Creek fauna. Bull. Amer. Mus. Nat. Hist., vol. li, pp. 59-210. [Equidæ from Snake Creek described, and discussion of phyletic relationships, pp. 153-175.]
- MATTHEW, W. D. 1924. A New Link in the Ancestry of the Horse. Amer. Mus. Novit. No. 131, Sept. 23, 1924. [*Platippus*.]
- MERRIAM, J. C. 1911. Tertiary mammal beds of Virgin Valley and Thousand Creek in Northwestern Nevada. Part II, Vertebrate faunas. Univ. Cal. Publ. Bull. Dept. Geol., vol. vi, pp. 199-304, pll. xxxii-xxxiii. [Descriptions of Tertiary Equidæ teeth and jaw fragments, pp. 256-266, figs. 24-36.]
- MERRIAM, J. C. 1913. Preliminary report on the horses of Rancho la Brea. Univ. Cal. Publ., Bull., Dept. Geol., vol. vii, pp. 397-418, 14 text figures. [Description of skull of *Equus occidentalis* and comparisons with other species.]
- MERRIAM, J. C. 1913. New Anchitherine horses from the Tertiary of the Great Basin area. Univ. Cal. Publ., Bull. Dept. Geol., vol. vii, pp. 419-434, 5 text figures. [*Hypobippus* and *Parabippus*.]
- MERRIAM, J. C. 1913. New Protohippine horses from Tertiary beds on the Western border of the Mohave desert. Univ. Cal. Publ., Bull. Dept. Geol., vol. vii, pp. 435-441, 4 text figures. [First report of Equidæ from the Barstow formation. Large collections from this formation subsequently obtained by Univ. Cal. and Mr. Childs Frick, not yet published.]
- MERRIAM, J. C. 1915. New species of the *Hipparion* group from the Pacific Coast and Great Basin provinces of North America. Univ. Cal. Publ., Bull. Dept. Geol., vol. ix, pp. 1-8, 5 text figures. [Four species based on teeth.]
- MERRIAM, J. C. 1915. New horses from the Miocene and Pliocene of California. Univ. Cal. Publ., Bull. Dept. Geol., vol. ix, pp. 49-58, 12 text figures. [Five species described, based upon jaws and teeth.]
- MERRIAM, J. C. 1915. Tertiary vertebrate faunas of the North Coalinga region of California. Trans. Amer. Phil. Soc., N. S., vol. xxii, art. 3, 44 pp., 49 text figures. [Chiefly discussion of correlation with marine Tertiary faunas.]
- MERRIAM, J. C. 1916. Relationship of *Equus* to *Platobippus*, etc. Univ. Cal. Publ., Bull. Dept. Geol., vol. ix, pp. 528-534, 18 text figures. [*Platobippus proversus* n. sp., intermediate between *Platobippus* and *Equus*, related to species from Blanco formation of Texas. (*P. proversus* subsequently referred by Matthew to *Platippus*).]
- MERRIAM, J. C. 1917. Relationships of Pliocene mammalian faunas from the Pacific Coast and Great Basin provinces of North America. Univ. Cal. Publ., Bull. Dept. Geol., vol. x, pp. 421-443, 1 text figure. [Correlation.]
- MERRIAM, J. C. 1919. Tertiary mammalian faunas of the Mohave Desert. Univ. Cal. Publ., Bull.

- Dept. Geol., vol. xi, pp. 437a-585, 253 text figures. [Revision of Barstow and Ricardo faunas, new material described. Equidæ pp. 472-505 and 548-568.]
- MERRIAM, J. C. 1925. (With Chester Stock and C. L. Moody.) The Pliocene Rattlesnake formation and fauna of Eastern Oregon, etc. Carnegie Institution Publ., No. 347, pp. 43-92, 45 text figures. [Equidæ teeth and jaws, pp. 71-81, figs. 26-35.]
- MITCHELL, S. L. 1826. Catal. Org. Rem. New York, pp. 7, 8. [First record of fossil horses in America.]
- OSBORN, H. F. 1889. The Mammalia of the Uinta formation, Part III, Perissodactyla. Trans. Amer. Phil. Soc., N. S., vol. xvi, part iii. [*Epibippus*.]
- OSBORN, H. F. AND J. L. WORTMAN. 1895. Perissodactyls of the White River beds. Bull. Amer. Mus. Nat. Hist., vol. vii, pp. 343-375.
- OSBORN, H. F. 1904. Evolution of the horse in America. Century Magazine, vol. lxi, pp. 3-17.
- OSBORN, H. F. 1904. Recent advances in our knowledge of the evolution of the horse. Science, vol. xix, p. 717.
- OSBORN, H. F. 1904. The evolution of the horse. Rep. Brit. Assoc. Adv. Sci., Cambridge, 1904, p. 607.
- OSBORN, H. F. 1904. New Oligocene horses. Bull. Amer. Mus. Nat. Hist., vol. xx, pp. 167-179, pll. iii, v, 7 text figures. [Good figures of skull and dentition of *Mesobippus* and *Misobippus*; several new species described.]
- OSBORN, H. F. 1905. Evolution of the horse. Recent discoveries and studies. C. R., 6e Cong. Int. Zool. Berne, p. 282.
- OSBORN, H. F. 1905. Origin and history of the horse. Address before the New York Farmers, Metropolitan Club, New York, Dec. 19. [Popular account of the origin of the modern breeds of horses and of the horse family in general.]
- OSBORN, H. F. 1912. Craniometry of the Equidæ. Mem. Amer. Mus. Nat. Hist., N. S., vol. I, pp. 57-100.
- OSBORN, H. F. 1913. The Horse Past and Present in the American Museum of Natural History and the Zoological Park. Irving Press, 4to.
- OSBORN, H. F. 1918. Equidæ of the Oligocene, Miocene and Pliocene of North America. Iconographic Revision. Mem. Amer. Mus. Nat. Hist., N. S., vol. II, pp. 1-117, pll. i-liv and 173 text figures. June 10th, 1918. [Systematic revision of all the American genera and species described from the Oligocene, Miocene and Pliocene with illustrations of all types previously described and many new species. Preceded by a correlation of the formations in which they are found. Many referred specimens figured and described.]
- OWEN, RICHARD. 1841. On *Hyracotherium leporinum*. Trans. Geol. Soc. London (2), vol. vi, pp. 203-208. [Earliest record of the four-toed horse, not then recognized as ancestral to the horse family.]
- OWEN, RICHARD. 1858. Description of a small Lophodont mammal (*Pliolophus vulpiceps*) near Harwick Qu. Jour. Geol. Soc. London, pp. 54-70. [Description of skull and jaws of *Pliolophus* (= *Hyracotherium*).]
- OWEN, RICHARD. 1870. On fossil remains of *Equus* from Central and South America. . . . Phil. Trans. Roy. Soc. London, vol. clx, pp. 559-573.
- PAS, L. VAN DE. 1909. Un Paso hacia adelante en el Camino de la Evolucion del Caballo. Anal. Mus. Nac. Buenos Aires (3), t. x, pp. 149-162. [Partial atrophy of the splints.]
- PAS, L. VAN DE. 1912. Otros Indicios de Evolucion Actual en el Caballo Criollo. Anal. Mus. Nac. Buenos Aires, t. xiii, pp. 397-411.
- PAVLOW, M. 1888. Etudes sur l'hist. paléontologiques des Ongulés, ii, Le développement des Equidæ. Extr. Bull. Soc. Imp. Nat. Moscow (2), vol. ii, pp. 135-182. [*Hipparion* excluded from the ancestry of the horse as a specialized side line.]
- PAVLOW, M. 1890. Etudes sur l'hist. paléontologiques des Ongulés, iv, *Hipparion* de Russie; V, Chevaux pleist. de la Russie, etc. Bull. Soc. Imp. Natur. Moscow, Ser. 2, vol. iii, pp. 653-716.
- PAVLOW, M. 1903. *Protobippus* en Russie. Bull. Soc. Nat. Moscow, 1903. [Foot bones referred to *Protobippus* (are more probably *Hipparion*. W. D. M.).]
- PAVLOW, M. 1915. Mammifères Tertiaires de la Nouvelle Russie. Mem. Soc. Imp. Nat. Moscow, N. S., t. xvii, livr. 4. [Pp. 18-35, pl. vi, description of *Hipparion* skulls, etc., from Russia.]
- PAVLOW, M. 1925. Nouvelle données scientifiques sur la position de l'*Hipparion*. Part 1, author's separate from? Bull. Soc. Nat. Moscow. [Review of various opinions upon phyletic position; author's conclusions to follow.]
- PETERSON, O. A. 1907. The Miocene beds of Western Nebraska and Eastern Wyoming and their vertebrate fauna. Ann. Carn. Mus., vol. iv, pp. 21-72, pll. ix-xix, 20 text figures. "Dec.,

- 1906," Mar. 21, 1907 (actual date of publication). [Skull of *Parabippus*, pp. 57-60, pl. xix.]
- PETERSON, O. A. 1920. Report upon the material discovered in the Upper Eocene of the Uinta Basin, etc., Ann. Carn. Mus., vol. xii, pp. 40-168, pll. xxxiv-xlvi. "Dec. 15, 1919," actual date of distribution appears to be June, 1920. [New *Epibippus* material pp. 101-3, pl. xliii; discussion of affinities of various other Eocene perissodactyls, pp. 103-140.]
- POCOCK, R. I. 1905. On the preorbital pit in the skulls of domestic horses and quaggas. Ann. Mag. Nat. Hist. (7), vol. xv, pp. 516-518.
- POMEL, A. 1897. Les Equidés. Pal. Monog. No. 12, Carte géol. de l'Algérie. Fontana and Cie, Algiers. [Algerian Pleistocene Equidæ.]
- RECHE, O. 1905. Ueber eine neue Equidenart aus der Pampasformation. Beitr. Pal.-Geol. Oest.-Ung., Bd. xviii, s. 225-241.
- ROTH, S. 1902. Nuevos restos de mamíferos de la Caverna Eberhardt en Ultima Esperanza. Rev. Mus. La Plata, t. xi, p. 37.
- ROVERETO, C. 1914. Los Estratos Araucanos y sus Fósiles. Anal. Mus. Nac. Buenos Aires, t. xxv, pp. 1-250.
- RÜTIMEYER, L. 1863. Beiträge zur Kenntniss der fossilen Pferde. Verh. natürl. Ges. Basel, Bd. iii, s. 558-696. [Extinct horses of Europe, chiefly Quaternary.]
- RÜTIMEYER, L. 1875. Weitere Beiträge zur Beurteilung der Pferde der Quaternär-Epoche. Mem. Soc. Pal. Suisse, t. ii.
- SCHLOSSER, M. 1903. Die fossilen Säugethiere Chinas. Abh. k. bayer. Akad. Wiss., 11, Cl. xii, Bd. I, s. 1-221, pll. i-xiv. [*Hipparion* and '*Anchitherium*' (= *Hypobippus*) from China; notes on phylogeny of Equidæ.]
- SCHMALTZ, R. 1905. Atlas der Anatomie des Pferdes. Berlin, 1905, 2nd ed., 1909. [Osteology of modern horse.]
- SCHWARZ, E. 1922. Notes on European fossil horses. Jour. Mammalogy, vol. iii, pp. 150-155. [Pleistocene horses of Eurasia grouped in two types, *E. stemonis* and *E. caballus*.]
- SCOTT, W. B. 1886. On some points in the evolution of the horses. Science, vol. vii, p. 13.
- SCOTT, W. B. 1891. On the osteology of *Mesobippus* and *Leptomeryx*. Jour. Morphol., vol. v, pp. 301-400.
- SCOTT, W. B. 1893. The Mammalia of the Deep River Beds. Trans. Amer. Phil. Soc., N. S., vol. xviii, No. 2. [*Mesobippus*, *Dumatippus* (= *Parabippus*), *Anchitherium* (= *Hypobippus*, *Protobippus* (= *Merychippus*)).]
- SCOTT, W. B. 1913. A History of Land Mammals in the Western Hemisphere. Pp. i-xiv, 1-693, 304 text figures. Macmillan, New York. [Semipopular treatise dealing with the New World mammals—outlines of methods of investigation, classification, osteology, distribution and faunas, and the phylogenetic history of the several orders. Equidæ, pp. 291-308.]
- SFVSB, J. 1912. Die fossilen Pferde Sudamerikas Kgl. Svenska Vetensk. Hand. Bd. xlviii. [Thorough critical revision of the South American Pleistocene Equidæ.]
- SELLARDS, E. H. 1916. Fossil vertebrates from Florida, etc. Eighth Ann. Rep. Geol. Sur. Fla., pp. 77-119.
- SINCLAIR, W. J. 1905. New or imperfectly known rodents and ungulates from the John Day series, Univ. Cal. Publ., Bull. Dept. Geol., vol. iv, pp. 125-143, pll. xiv-xviii. [Skull of *Mesobippus*.]
- SINCLAIR, W. J. 1915. Additions to the fauna of the Lower Pliocene Snake Creek beds. Proc. Amer. Phil. Soc., vol. liv, pp. 73-95.
- SINCLAIR, W. J. 1925. The mounted skeleton of a new *Mesobippus* from the Protoceratops beds. Proc. Am. Phil. Soc., vol. lxiv, pp. 55-63, pl. iii.
- SISSON, S. 1910. Textbook of Veterinary Anatomy. Philad.
- SOERGEL, W. 1911. Die Pferde aus der Schotterterrasse von Steinheim a. d. Murr. Neues Jahrb. Beil. Bd. xxxii, s. 740-761, pll. xxiii-xxv.
- STREHLIN, H. G. 1903-6. Die Säugethiere des schweizerischen Eocäns. Parts i-iii. Perissodactyla. Abh. Schw. Pal. Gesell., Bd. xxx-xxxiii. [Revision of European Eocene Perissodactyla and correlation with American Eocene genera.]
- STROMER VON REICHENBACH, E. 1911. Die einstige Verbreitung afrikanischer Säugethiere. Naturwiss. Woch., vol. x, pp. 814-816.
- STUDER, TH. 1911. Eine neue Equidenform aus der Obermiocän von Samos. Vortrag. 21 Jahresversam. Deutsch. Geol. Ges. in Basel. [*Hipparion* "*proboscideum*," interpretation of the facial pits as pockets lodging powerful facial muscles, hence presumably a proboscis.]
- TROUWART, E. 1913. Did the horse exist in America before this continent was discovered by Europeans. Sci. Amer. Suppl. vol. lxxvi, p. 387. [Extinct in Pleistocene.]
- VILLADA, M. M. 1903. Apuntes acerca de la fauna fósil der Valle de México. Anal. del Mus. Nac. de Mex., t. vii, pp. 41-451.

- WERTHOFFER, M. 1888. Beiträge zur Kenntniss der Fauna von Pikermi. Beitr. Pal.-Geol. Österreich., Bd. vi.
- WINGE, H. 1906. Jordfundne og Nulevende Hovdyr (Ungulata) fra Lagoa Santa . . . Brasilien . . . E. Museo Lundii, Kjøbenhavn, pp. 3-239, 9 plates. [Teeth and feet of *Equus* from Brazil; critical review of literature on extinct Equidæ.]
- WORTMAN, J. L. 1882. On the origin and development of the existing horses. Kansas City Rev. Sci. and Industry, vol. v, pp. 719-726, vol. vi, pp. 67-75.
- WORTMAN, J. L. 1896. Species of *Hyracotherium*, etc. Bull. Amer. Mus. Nat. Hist., vol. viii, pp. 81-110. [Revision of the species of four-toed horses from the Lower Eocene of America.]
- WÜST, E. 1900. Untersuchungen über das Pliocän und das älteste Pleistozän Thüringens . . . Abh. naturf. Ges. Halle, Bd. xxiii, pp. 16-368. [Early Pleistocene species of *Equus*.]
- ZITTEL, K. A. v. 1923. Grundzüge der Paläontologie. 4te Aufl. Neuarbeitet von F. Broil. u. M. Schlosser. II Abtheilung Vertebrata, R. Oldenbourg, München u. Berlin. [Equidæ, pp. 540-550. Review of the fossil record with concise diagnoses of the extinct genera, mention of most of the species and occurrence.]
- ZITTEL, K. A. v. 1925. Textbook of Palæontology, vol. iii, Mammalia. Revised by Schlosser and Woodward. Macmillan. London. [The translation is from an earlier edition than Zittel 1923 supra, Equidæ, pp. 144-158.]





RECENT RESULTS RELATING TO CHROMOSOMES AND GENETICS

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THE success of the method of interpreting genetic results in terms of a chromosome mechanism must be apparent to any one who has followed the literature of recent years. This is not only true of the mechanism as applied to Mendel's law of heredity, but also to many of the novel situations that are continually presenting themselves where a strict, and in some cases even a predictable, parallel has been found between new genetic occurrences and an alteration in the chromosomal mechanism.

In the following pages three lines of recent advance will be discussed; first, the evidence relating to an increase in chromosome number and its bearing on the problem of a permanent change in the number of the chromosomes; second, the evidence of sex-chromosomes in dioecious plants, and the interpretation of sex in terms of genes; third, the evidence relating to the "emptiness" of the Y-chromosome.

MULTIPLE CHROMOSOME GROUPS

Recent discoveries have shown that species belonging to the same genus sometimes differ from each other in that their chromosome numbers are multiples of some basal number which is the gametic or haploid number of the lowest member of the series. It is tempting to interpret these polyploid series as having arisen by the doubling, trebling, quadrupling, etc., of the number of chromosomes. There can be no doubt but that this is the correct

interpretation in particular cases, but the observations have now gone far enough to show that it is unsafe to reconstruct all polyploid series on the assumption that they have arisen in this way. When the evidence from pedigree cultures suffices to show that a fourfold type has arisen directly from a diploid type, there can be no doubt but that the same set of chromosomes is present in fourfold number in the tetraploid, but without this direct evidence it is unsafe to conclude that a double chromosome type of one species has necessarily arisen from a related species by a direct process of doubling.

The characters shown by those diploids, triploids, tetraploids, that have arisen in pedigree cultures may be ascribed to the differences in their chromosome numbers, but when the differences in numbers have come about in other ways, as by hybridizing, for instance, the situation is more complex, and the characters may be due, in part, to the differences in the number of the chromosomes and in part, to the combined effects of the chromosomes of different kinds brought together in the hybrid. The problem is further complicated by the relative volumes of the cytoplasm in cells with different numbers of chromosomes, since this involves questions relating to the influence of the chromosomes on the amount of protoplasm present in the cells, and the subsequent effect of the chromosomes on this amount.

These considerations are not merely *a priori* possibilities but have arisen in connection with recent work on chromosome numbers and have been much discussed in recent literature of genetics and cytology. For example, there can be little doubt that the differences in characters between the diploid and tetraploid evening primrose are primarily due to differences in chromosome numbers. The same statement may be made for the diploid and tetraploid *Datura* and for the diploid and tetraploid tomato and nightshade. In the polyploid series of roses that have recently been studied by Täckholm, by Harrison and Blackburn and by Hurst, there is evidence that some of the polyploids may be multiples of a basal type, while in other cases, there is evidence from the characters of the roses themselves, as well as from the behavior of their chromosomes at the maturation divisions, that the increase in number of chromosomes may have come about through crossing between different species. Hurst in particular has brought forward evidence in support of his view that five distinct varieties (or species) are at present combined in different ways in the roses of the Canina section. This evidence is so interesting that a somewhat more detailed statement may be given.

Hurst thinks that the Canina roses can be referred to five primary groups or species that are now combined as tetraploids, hexaploids, octoploids, etc. These polyploids, he thinks, are not to be regarded as multiples of the primary types, but rather as composite forms produced perhaps by hybridization. It is true that Hurst finds certain geographical difficulties in ascribing a hybrid origin to these roses, and suggests that the lower numbers of the series with fewer chromosomes have arisen through the loss of groups of 7 chromosomes each, but this

interpretation is difficult to bring into line with the known behavior of chromosomes in the maturation divisions of eggs and sperm. On the other hand, other evidence from the work of Harrison and Blackburn and from the cytological evidence by Täckholm indicates, that some of the polyploid roses have arisen by doubling of a basal set of chromosomes. For instance, Täckholm finds that the smallest number, present in some species, is 14 (diploid) chromosomes. There are others that are tetraploids (28), others hexaploids (42), and others that are octoploids (56). Some of these groups are represented in figure 1. In those cases where the increase in numbers has arisen directly by doubling or quadrupling the diploid number, it is to be anticipated that at the time of conjugation of the chromosomes each chromosome will find a mate (or else like chromosomes will mate in fours) and consequently at the reduction division they will separate and pass to opposite poles leaving no unmated, "single" or lagging chromosomes on the spindle. Those roses whose chromosomes are in pairs in the maturation stages (of the pollen) are interpreted by Täckholm as having arisen by doubling. On the other hand the maturation divisions of other roses give a different picture. For instance, seven chromosomes may pair with seven, leaving fourteen unpaired (single) chromosomes lagging on the spindle. The simplest interpretation in such cases is that the fourteen single chromosomes have had a different origin from the fourteen that conjugate. In other species there may be again seven paired and in addition twenty-one singles, and in still others seven paired and twenty-eight singles, etc. It seems not unreasonable to suppose that the fourteen chromosomes that conjugate to give seven pairs are in all

cases members of one species, while the additional 14 or 21 or 28 have come from another species and have been brought together through hybridizing. If this is the correct interpretation, polyploid species may arise within the same genus either by doubling, quadrupling, etc. of the same set of chromosomes, or by the addition of foreign sets.

It is clear that an understanding of these relations must have an important bearing on the genetics of these roses when these combinations have been further worked out.

himself points out, the chromosomes, even in species having the same number, may have different size relations, and the nuclear diameters (resting stages) do not always bear a constant relation to the number of chromosomes present.

In different species of clovers (*Trifolium*) the following chromosome numbers (diploid) have been recently reported by Karpetschenko. Eight species have 14 (fig. 2), eleven have 16, one has 32, one has 48, one has about 80, one has about 130. If the haploid number be taken as eight, then four of the series are multi-

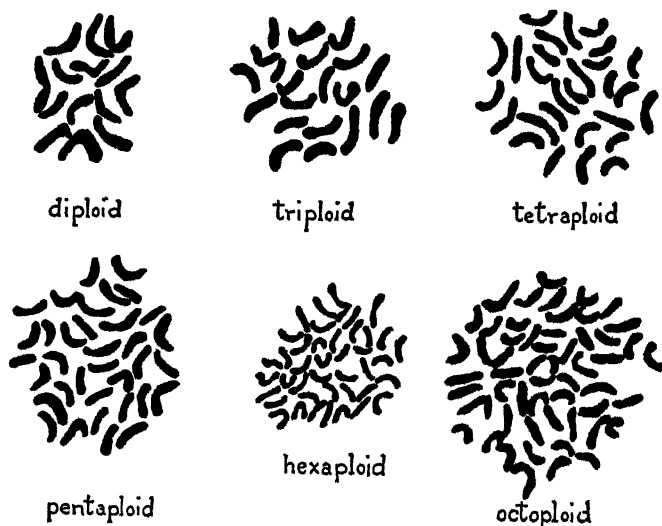


FIG. 1. CHROMOSOME GROUPS FROM DIPLOID CELLS OF DIFFERENT SPECIES OF ROSES
(After Täckholm)

The danger of erroneously interpreting all polyploid series in terms of multiples of a basal chromosomal number is also obvious when other groups of species are considered, in which, while some forms may be ranged as multiples of an assumed basal number, others are just as obviously not such multiples. A few such instances may be cited by way of illustration. In the cultivated varieties of chrysanthemum, Tahara finds varieties with 9, 18, 27, 36 and 45 chromosomes, but as he

ples of this number, namely 16, 32, 48, 80. The highest number (130) is only approximately correct, if it had two less (128) or six more (136) it would fall into the series. The smallest number (14) that is present, in about one-third of the series, stands apart from the rest of the species. It could arbitrarily be derived from the 16 type by the union of two chromosomes, or the 16 type could be derived from the 14 type by the breaking apart of two chromosomes of the latter,

but there is nothing in the sizes or shapes of the chromosomes to warrant this assumption. Bleier has also recently made a study of chromosome numbers in several species of clovers. Four species examined by him had 14, eight species had 16, one species had 18, two species had 28, two had 96-98. In this account the numbers 14, 28 and 98 (?) might possibly be interpreted as multiples of 7, while 16 and 96 (?) might be interpreted as multiples of eight. Taking Karpetschenko's and Bleier's results together, assuming the numbers to be substantially correct

the size in one species may be double that of another species, in other cases, the number may be doubled but the size remains the same, or the number as well as the size of the chromosomes may be six or seven fold as great. It is evident, as Bleier points out, that from these relations the differences in numbers must sometimes have arisen in different ways.

Heilborn also sounds a note of warning against the arbitrary arrangement of chromosome numbers in series of multiples in a phylogenetic sense. In the sedges, *Carex*, there are many differences in chro-

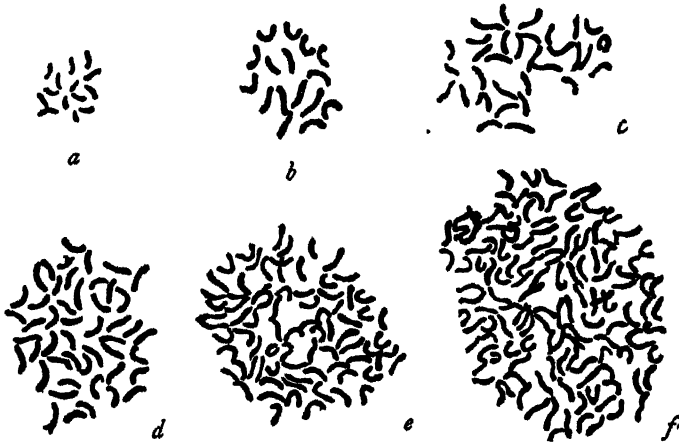


FIG. 2. CHROMOSOME GROUPS OF SOMATIC CELLS OF DIFFERENT SPECIES OF CLOVERS (*TRIFOLIUM*) WITH 14, 16, 32, 48, 80, AND 130 CHROMOSOMES

(After Karpetschenko)

(they do not always agree), a case for two series, multiples of 7 and 8 respectively, might be made out, but there are several further considerations that make such a generalization of doubtful value. For instance, Bleier, who has studied especially the reduced groups (gemini) points out that while, in some species the number and size of the chromosomes may be the same, in other species, the number of chromosomes may be the same but their sizes different. A comparison of still other species shows that while the number of the chromosomes as well as

mosome numbers. For example, it is possible to pick out species that may appear to have chromosome numbers that are multiples of three as a fundamental haploid number, thus 9, 15, 24, 27, 36, and 42 chromosomes. It is also possible to put together a series that has four as a fundamental number, thus 16, 24, 28, 32, 36, 40, and 56 chromosomes and still others that are multiples of seven, thus 28, 35, 42, and 56. Several of these numbers appear in two or more of the series. Furthermore the size relations in certain cases are not consistent with the assumption

that the higher numbers are simple multiples of the lower. There can be little doubt that the solution of the problem can not be found in such a simple fashion. That polyploidy may in some cases play a rôle in the production of the hybrid numbers of chromosomes can scarcely be denied, but that all cases of multiples are in themselves evidence of polyploidy is clearly not true. Other evidence of a different sort will be required in each case before it can be interpreted in relation to the others. The genus *Crepis* is one of the earliest in the plant series whose chromosome numbers aroused interest, both because the small number present made exact counts possible, and also because different numbers, sometimes multiples of each other, are present. Rosenberg recorded species with 3, 4, 5, 8, and 20 pairs. Marchal recorded species with 3, 4, 5, 6, 8 and 16 pairs, and suggested that four is the basal number for the group; those that are not complete multiples being accounted for as due to bipartition of single chromosomes or to the doubling of certain pairs—a procedure that has come to be looked upon in recent years with some scepticism. Miss Mann has recently reported one species of *Crepis* with 6 chromosomes ($n = 3$), seventeen with 8 chromosomes ($n = 4$), five species with 10 ($n = 5$); one with 16 ($n = 8$); one with 18 ($n = 9$), and one with 40 ($n = 20$). While a basal number four will serve for some of these species, other species are not multiples of this number. Measurements of the chromosomes of several species, that have been made by Miss Mann, do not give much further insight into the possible interrelationships between the chromosomes in this genus.

THE ADDITION OF SINGLE CHROMOSOMES

In most animals and plants the diploid or double number consists of pairs and is

therefore an even number. The exceptions to this rule are those cases where one sex has one less chromosome than the other. On rare occasions an additional member of one pair may appear giving three of a kind. These are called trisomic or triploidy forms. The first case of the kind was observed in *Oenothera*, where 15 chromosome plants were found. Later, other cases were recorded, for example, in *Drosophila* and in *Datura*. The way in which such a condition is reached is fairly well understood. At the maturation of a germ cell, two daughter chromosomes, that ordinarily would pass to opposite poles of the mitotic spindle and then go to separate cells, fail to separate completely and get caught in one cell, which comes, in consequence, to contain one additional chromosome. If such a germ cell unites with one of the opposite sex, an individual is produced that has one more chromosome than the normal type. The presence of an additional chromosome does not appear to act favorably on the individual in the cases so far observed. The normal balance of the genes, that is adjusted to produce a viable type, is upset with more or less serious results. The evidence, as far as it goes, does not seem favorable, therefore, to the view that new self-perpetuating types could be established in this way. Moreover such heteroploid types, when bred to the normal type, transmit their combination to only half of the offspring. The chance is, therefore, that in time they would be eliminated on both counts.

There is, however, something further to be said in this connection. If the extra chromosome in question is a small one, like the fourth chromosome of *Drosophila*, the balance may be little disturbed and the characters little affected. In other cases, where a larger number of chromosomes than in *Drosophila* is present, the

addition of one new member may also be less injurious. Moreover if polyploidy has already taken place the addition of a new member might less seriously affect the viability since the balance of the genes is less disturbed.

The occurrence of a type with one additional chromosome furnishes theoretically the possibility of producing from it a type with two additional chromosomes, i.e., four of one kind, or a tetra-type or tetrasomic type. Such a type, other things being equal, might seem to give an opportunity to produce a new type with an additional pair of chromosomes. If the tetrasomic type belongs to a monoecious species, i.e., one that produces both eggs and pollen grains, self-fertilization will give, in one-fourth of the offspring, individuals with two extra chromosomes, and there will be an even number of chromosomes to conjugate. But the balance of the genes will then be still further disturbed than in the trisomic type, and the expectation is that the result will be more injurious even than when only one chromosome is added. In the few instances of the sort that are known, viz., *Oenothera* and *Datura*, the evidence gives little encouragement for the view that, by the addition of two extra chromosomes, new types may be established.

The loss of a member of a pair of chromosomes also produces an uneven number of chromosomes. Such a result may be more injurious to the individual than the addition of one chromosome, and if, through such a condition, the further loss of the other member of the pair results, which is theoretically possible, the evidence indicates that the effect will generally be fatal to the life of the individual. Thus while the loss of one of the smallest chromosomes of *Drosophila* can be borne the loss of both small chromosomes seems to be fatal. At least,

no such individuals have as yet been found under conditions that would lead to the formation of such combinations, namely, by mating two individuals each with only one of the fourth chromosomes.

There remains for consideration the possibility that an increase in the number of chromosomes may come about through the breaking apart of one or more chromosomes. In fact there are numerous cases on record where broken chromosomes have been detected in cells, and other cases where one or even all the chromosomes may break apart as a regular procedure. This may seem to give a better chance for establishing new numbers. If one chromosome should become broken into two parts early in the germ track, many germ cells might come to contain the broken parts. In a monoecious plant that is self-fertile, a new individual arising by the union of two such cells would contain four pieces, instead of the usual two chromosomes, and if these pieces behaved normally in division, a new type with the same number of genes as the original, but with two more chromosomes, would result. But there is an obvious objection to such a simple solution. The chromosomes are attached to the poles of the spindle by achromatic fibres that arise from or are connected with specific regions of each chromosome. It is uncertain whether both pieces of a broken chromosome could move (or be carried) to the poles of the spindle as do normal chromosomes. At least, until evidence on this score is available, it is hazardous to build up a theory on the assumption that cell division would be normal.

The problem is even more complex in forms with separate sexes where the broken chromosome pieces would have to be carried along through successive gen-

erations until like met like—an improbable, although a possible event. Since no advantage is supposed to arise from the separation, and possibly some disadvantage in mitosis, as stated above, it does not seem likely that such a condition would be self-perpetuating.

There remains another possibility, namely, that a bent chromosome might break apart at the attachment point of the spindle fibre and each part might then

in which on four occasions the two straight X-chromosomes became united at one end to form a V-shaped chromosome. This process, to be sure, does not give a type with one less chromosome, since the two united chromosomes take the place of the two single ones in the female, and the male then gets his single X from his father. The two united X's may break apart, and usually at the point of union. Here we have proof that union

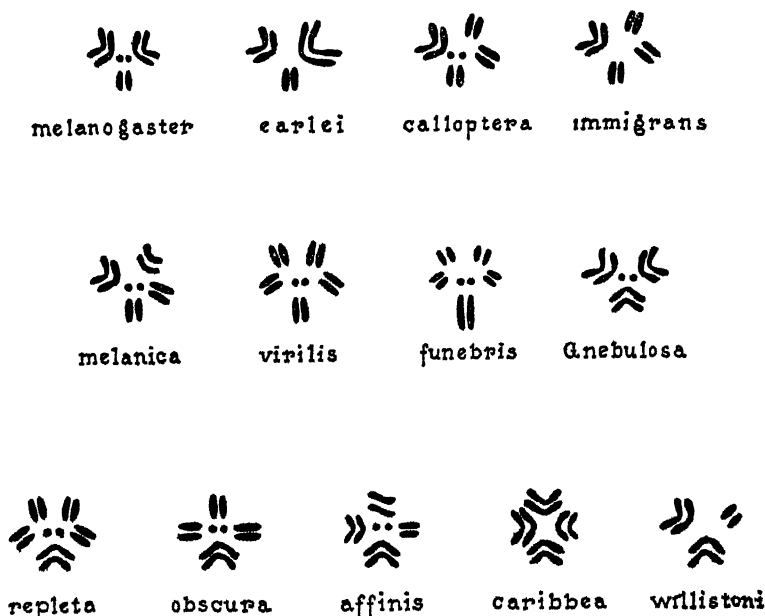


FIG. 3. DIAGRAM OF FEMALE CHROMOSOME GROUPS (DIPLOID) OF DIFFERENT SPECIES OF *DROSOPHILA*;
THE PAIR OF X-CHROMOSOMES IS THE LOWERMOST PAIR IN EACH GROUP

(After Metz and Moses)

possess a spindle-fibre attachment of its own. This might seem more probable if the bent chromosome had been formed by a previous union of two chromosomes uniting at their spindle-fibre ends. In fact, there is one known case in which two chromosomes (with known mutant genes) became attached to each other. On rare occasions the two may again separate and then one part at least is known to behave as a normal single chromosome. The case referred to is that of *Drosophila*

and separation of two chromosomes may take place, but the situation is unique and its general application may seem doubtful. Nevertheless the result invites a comparison between the shapes of the chromosomes in different species of *Drosophila* where some species have two pairs of straight rods that may be, and have been, in fact, compared with a single pair of bent chromosomes of other species. Metz has brought together in a diagram (fig. 3) the diploid chromosome groups of

different species of Drosophilidae. Inspection of these groups will show how easily some of them may be converted into others by supposing that two pairs of chromosomes have united, or contrariwise by supposing that a pair has become separated into two pairs. It is



FIG. 4. DIAGRAM OF MALE CHROMOSOME GROUPS OF *DROSOPHILA MULLERI* AND *D. REPLETA* (After Metz and Moses)

quite possible that this is the explanation in some cases, but the risk involved in any such arbitrary procedure may be illustrated by a single instance from the figures given. Two species, *Drosophila*

an autosome could have come from since the same number of autosomes is present in both species.

Delaunay has recently made direct comparison between species of plants belonging to the two genera *Bellevia* and *Muscari*. In the former there are in some species eight chromosomes each sharply bent giving a longer and a shorter arm (fig. 5). In the latter there are species with sixteen straight chromosomes whose sizes seem to correspond to the parts of the bent chromosomes of the *Bellevia* group. Delaunay thinks that the transition from one genus to the other is brought about by the simple process of separation of the bent chromosomes into their component parts, but from the point of view of the genes it is not apparent how a simple separation could be the immediate cause of the change in the character of the plants, nor does it seem probable that such

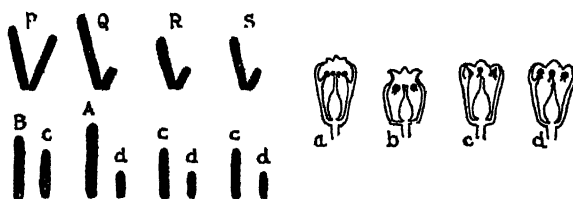


FIG. 5. BENT CHROMOSOMES OF *BELLEVIA* (ABOVE TO LEFT) AND OF *MUSCARI* (BELOW) The first two flowers to the right are *Muscari*, the second two are *Bellevia*. (After Delaunay)

repleta and *D. mulleri* are so closely alike that they "were reared in the laboratory under the same name until it was found that they differed in their chromosomes and that they would not hybridize." Subsequently they were differentiated by several external characters. Both species have the same number of chromosomes (fig. 4) but in *repleta* the X-chromosome is bent and in *mulleri* it is straight. In the former the bent X is about twice as long as the straight X in the latter. If the bent X's be supposed to have arisen by the union of an X chromosome with an autosome, it is not apparent where such

a separation would occur simultaneously in all the bent chromosomes at the same time. Granting that the two chromosome groups may, in some of the species at least, bear the interpretation that Delaunay has put upon them, it may appear that other change and perhaps changes in genes may be the more immediate cause of the differences in the characters of the different species.

THE ESTABLISHMENT OF NEW CHROMOSOME NUMBERS BY HYBRIDIZING

Another way in which types with new chromosome numbers may at times arise

is indicated by the recent work of Ljungdahl, and of Clausen and Goodspeed, who have produced, by crossing, types with stable chromosome numbers different from the original parental ones and multiples of a basal number common to those types. A poppy, *Papaver nudicale*, having 14 chromosomes ($n = 7$) was crossed to *P. striatocarpum* having 70 chromosomes

to one of the parental types it may be possible to produce tetraploid, and octoploid types.

Whether the poppies used in this cross are to be ranked as varieties or species is uncertain, but it is evident that since one type brings in only seven chromosomes, and since there are twenty-one conjugants in the hybrid, some of the pairs

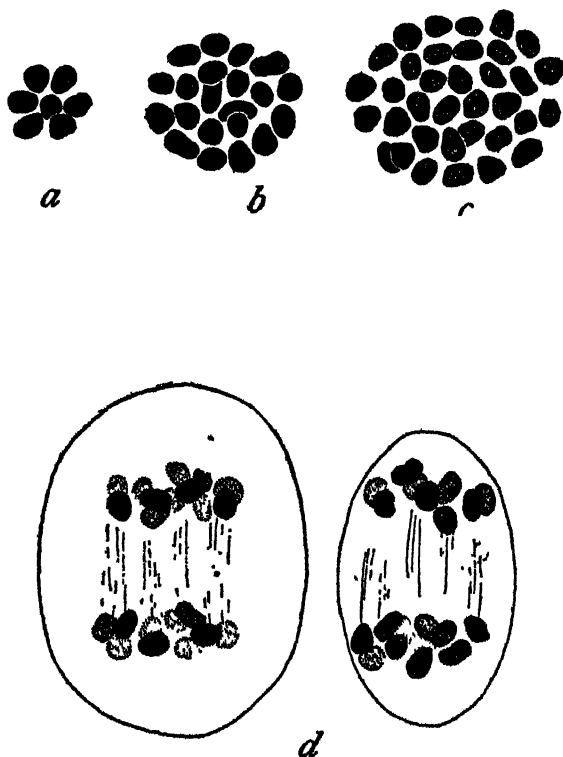


FIG. 6. *a*, CHROMOSOME GROUP (GEMINI) OF *PAPAVER NUDICALE* WITH SEVEN GEMINI (DIPLOID 14); *b*, OF *P. STRIATOCARPUM* WITH 35 GEMINI (DIPLOID 70), AND *c*, OF HYBRID WITH 21 GEMINI (DIPLOID 42).

Below are two sections of the same dividing sperm-mother-cell without any lagging chromosomes. (After Ljungdahl.)

($n = 35$). The hybrid has 42 chromosomes (fig. 6) and is fertile. When its germ cells mature there are 21 paired chromosomes (gemini), that separate at the first division (fig. 6*d*), 21 passing to each cell. No single chromosomes and no irregularities are present. A new type, a hexaploid, with 42 chromosomes has been produced. By backcrossing such a type

must be made by union of the chromosomes of one type with those of the other, while the remaining conjugants must be formed by the union of chromosomes from the parent with the larger number.

Another remarkable case has recently been reported by Clausen and Goodspeed in which a stable type with a new number of chromosomes has been formed from

two undoubted species of tobacco. The two species *Nicotiana glutinosa* and *Tabacum* generally give, when crossed, a weak hybrid that produces only a few viable seeds after self-fertilization. Three such hybrids were obtained, one of which was partially fertile after hand-pollination. It produced numerous F_2 offspring, most of which were fairly fertile. One of the F_2 plants was more robust than the others. When its chromosomes were studied, 36 bivalents were found to be present. The somatic number, therefore, must be 72 which is exactly twice the number (36) present in the first generation (F_1) hybrids formed by the union of 12 chromosomes from *glutinosa* and 24 from *Tabacum*. The result may be interpreted to mean that a doubling of all the chromosomes had occurred immediately after fertilization in one of the F_1 hybrids. Such an occurrence would bring about a diploid condition in each set of chromosomes, and hence a composite tetraploid with respect to the sum total of its chromosomes. The new type then, contained 24 *glutinosa* chromosomes ($12 + 12$) and also 48 *Tabacum* chromosomes ($24 + 24$). There would be expected to be present in the maturation stages of this F_1 plant two of each kind of chromosomes, which, mating in pairs, would give the recorded number of 36 bivalents. The observed regularity of the reduction division in this tetraploid hybrid is in accordance with this view, especially when contrasted with the irregularities observed in the ordinary F_1 individuals having 36 chromosomes where there are numerous unpaired chromosomes that are distributed irregularly.

Thus a new hybrid type with a new chromosome number, that is expected to breed true to its hybrid characteristics, has been produced from a cross of two undoubted species. Clausen and Goodspeed point out that the same explanation

may be applicable to the tetraploid *Primula kewensis*, a hybrid of *P. floribunda* and *P. verticillata*. The original hybrid was sterile but it produced a bud sport that gave rise to the constant form known as *P. kewensis*. Each of the original species had 18 chromosomes (haploid 9): the sterile hybrid had 18, and *P. kewensis* 36 chromosomes. The latter may be supposed to have arisen by a somatic doubling of the 18 chromosomes present in the hybrid, and as a result there would be two of each of the original kinds of chromosomes in the bud sport that gave rise to *P. kewensis*. It is, then, a hybrid tetraploid breeding true to its double chromosome composition.

SEX AND SEX CHROMOSOMES IN FLOWERING PLANTS

The recent discovery of a pair of differential sex chromosomes in several dioecious flowering plants has aroused much interest. In animals the main facts connected with the sex mechanism are well known and a review of the evidence is unnecessary, but in plants the facts are so new that a brief summary of recent work may not be out of place.

The simultaneous announcement in 1923 by three independent investigators that a differential pair of chromosomes occurs in certain dioecious plants came as a surprise because sex chromosomes had been often looked for in plants but not discovered. Santos examined the dioecious plant *Elodea* and found in the male an unequal XY pair of chromosomes (figs. 7 and 8) besides the 44 autosomes. Two kinds of pollen grains result, one with X (and 22 autosomes) the other with Y (and 22 autosomes). The chromosomes of the female were at that time not recorded but the occurrence of an unequal pair in the male plant and their segregation in different gametes made

their interpretation as sex chromosomes very probable. A year later (1924) Santos reported a pair of sex chromosomes in the female of *Elodea* that were equal in size (fig. 8) and corresponded to the larger member (X) of the XY pair in the male.

opposite pole. This was confirmed a year later by Sinoto ('24). Two kinds of pollen grains result, presumably sex differentiating. Another botanist, Winge, reported at the same time an unequal pair of chromosomes in the male hop-plant

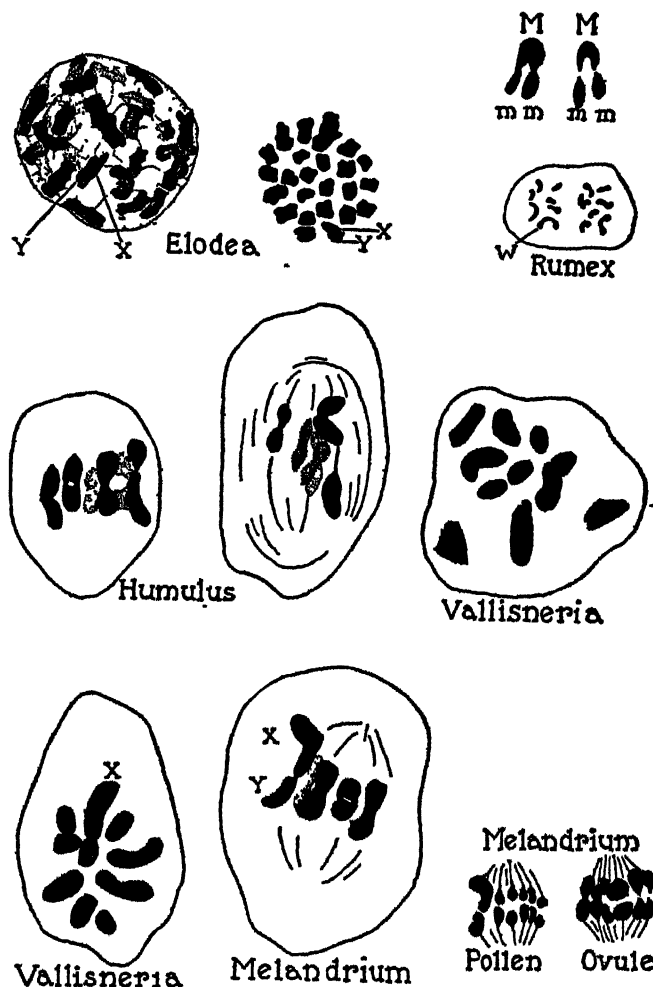


FIG. 7. SEX CHROMOSOMES (X AND Y) IN SEVERAL DIOECIOUS FLOWERING PLANTS
(After Belär)

Two cytologists, Kihara and Ono have found two small chromosomes and one large one in the male of *Rumex* that come together at the maturation of the pollen mother cells (fig. 7) and then separate, the two smaller going to one pole and

(fig. 7) and also in *Melandrium*. He also found in *Vallisneria* an unpaired chromosome (X) in the male. In the latter case, half the pollen grains have one X (and eight autosomes) and half no X (and eight autosomes).

equal pair of chromosomes in the male of *Melandrium*, (fig. 7) and has also a further fact essential to complete the chain of evidence, namely, that in the female there is an equal pair of corresponding

that the two chromosomes in the female correspond more nearly to the size of the larger (X) chromosome of the male.

Blackburn and Harrison reported that an unequal pair of chromosomes is present

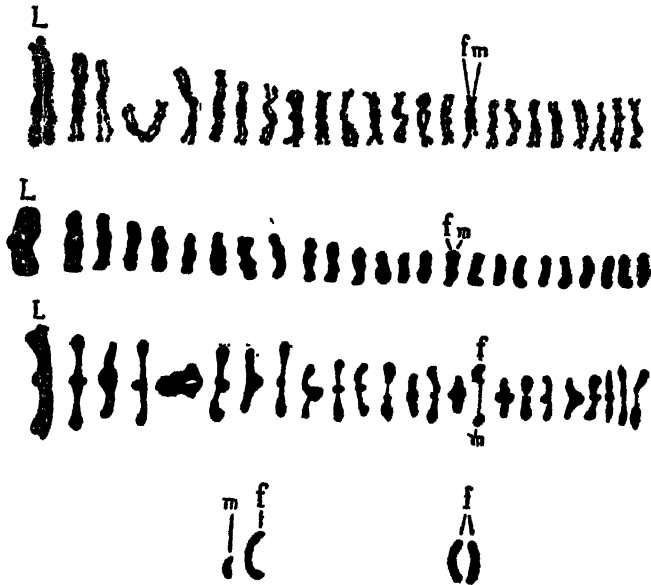


FIG. 8. PAIRED CHROMOSOMES (GEMINI) OF *ELODEA* (MALE)

The two upper lines include the XY pair (*f* and *m*) in conjugation; in the third line they are in process of separation. In the fourth (lowest) line the difference in size between X and Y (here *f* and *m*) in the male is shown to the left, and the two X's (of the same size) are shown to the right. (After Santos)

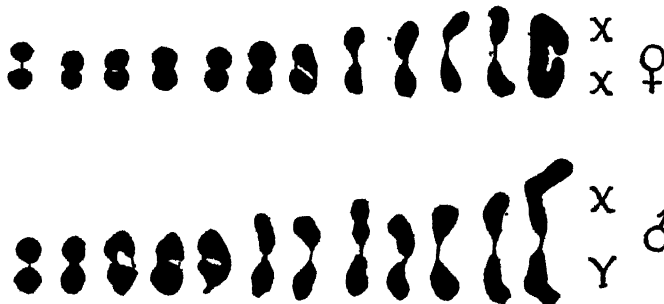


FIG. 9. TWELVE CHROMOSOME PAIRS (GEMINI) OF *MELANDRIUM ALBUM*; THOSE FROM FEMALE IN THE UPPER LINE WITH X-X PAIR; THOSE FROM MALE IN LOWER LINE WITH X-Y PAIR (After Meurman)

chromosomes. She thought it probable that the two chromosomes in the female correspond to the smaller (Y?) chromosome of the male but the more recent observations of Meurman (fig. 9) indicate

in the male of the poplar (*Populus tremula*) and in the male of a willow (*Salix viminalis*).

Hirata found in one race of hemp (*Cannabis sativa*) an unequal pair of

chromosomes, although McPhee had failed to discover such a difference in the variety of hemp studied by him. These results with hemp are interesting since it has been shown that environmental conditions have an effect on the development of male and female flowers on the same plant, at least in certain races. Yampolsky reports that in *Mucurialis* there is not an unequal pair of chromosomes in the male.

The latest report on the subject by Meurman adds a number of other cases to this list for the male, and confirms several of the earlier results. In three species of poplar he reports an unequal pair in the male. He finds the same relation in *Valeriana* and probably in *Urtica* and in two varieties of *Melandrium* (fig. 9). A tripartite chromosome is present in the male of two species of *Rumex*. In one species of *Dioscorea* (*D. sinuata*) there is probably an unpaired chromosome in the male, and two classes of pollen with 17 and 18 chromosomes were observed in one case in sister "plates." In another species no inequality in the pair could be observed. In six other dioecious plants no inequality in any of the chromosome pairs could be detected.

These observations go far towards establishing the view that there exists in some dioecious plants a chromosome mechanism that determines sex. The male is digametic in all cases so far described as earlier experiments by Correns and by Shull had made probable. The mechanism is the same in kind as the XX-XY type in many insects. It should be pointed out with all possible emphasis that this correspondence in mechanism does not necessarily mean that the two processes are comparable as to the genes involved. Only if sex is generalized and supposed to be in all cases the result of the same specific sex-genes that are com-

mon to all organisms could there be any grounds for such an assumption. There is as yet no evidence of specific genes that have to do with sex determination alone and least of all any grounds for such an assumption when for example a flowering plant and an insect are compared. The evidence seems rather to mean that a certain balance between sets of genes, possibly a very large number, inclines the individual to develop the male sex-cells, while another balance tips the scale another way. It is quite possible that there is not one way in which the scale may be tipped but many ways. If so, sex-determination in the flowering plants may be due to different sets of genes from those that determine sex in animals.

SEX IN HAPLOIDS

The demonstration by Allen in 1919, that the cells of the female haploid gametophyte of the liverwort, *Sphaerocarpos*, have a large X-chromosome and that the cells of the male haploid gametophyte have a corresponding small Y-chromosome, gives a reasonable explanation of the differences shown by their prothallia (gametophytes). Similarly the experimental demonstration by the Marchals, by Wettstein and others that from each spore-mother-cell of dioecious mosses arise two spores that develop into female protonemata (gametophytes), and two other spores that develop into male protonemata (gametophytes), falls into line with Allen's results on the allied liverworts. It is customary to speak of the two kinds of gametophytes as female and male respectively since one produces eggs the other sperm cells (antherozoids). The succeeding generation, the sporophyte (zygote) arising from the fertilization of the egg by the sperm, is sometimes said to be sexless or asexual. It has however one X- and one Y-chromosome.

Some unnecessary confusion has arisen between the terminology used for the moss and liverwort and that employed for dioecious flowering plants in which the terms female and male apply to the sporophyte (diploid) generation and not to the egg cell (which is a part of the haploid generation within the embryo sac) and to the pollen grain (which is also a part of the haploid generation). It may seem at first sight, that male and female are used in these two groups in a different sense. There is no real contradiction, however, except a verbal one arising from phylogenetic implications. If the two cases in question are stated in terms of genes, the imagined difficulties disappear. In the liverworts, for instance, the balance of genes in the haploid gametophyte, containing the large X-chromosome, leads to the production of egg-cells and the balance of genes in the haploid gametophyte containing the small Y-chromosome leads to the production of sperm-cells. The egg-bearer is here called female, the sperm-bearer is called male. In the diploid generation of those flowering plants that are dioecious, where a differential pair of chromosomes is present in the male, the balance of the genes in the diploid generation between the autosomes and two X's gives a female (an individual that produces eggs), and the balance of the genes in the diploid generation between the autosomes and the XY pair gives a male (an individual that produces sperm cells). Both in the liverwort and in the flowering plant the situation turns on a balance between sets of genes. It may be that the same sets of genes are not involved in both cases, or that some of them are the same, others are different. The essential point is that in both cases, differences in balance lead to two kinds of individuals which are called males and females since they produce eggs and sperm cells respectively.

In criticism of these statements it may possibly be said that the facts have only been restated and not explained. This is quite true. All that has been attempted is to point out that the facts may be restated in such a way that there is no apparent contradiction involved in the two cases. We may look forward perhaps to the time when the number and nature of the genes involved in cases where a difference in balance produces two kinds of individuals, will be determined. Meanwhile there is nothing in the situation that need cause anxiety, and certainly nothing that can be used as a refutation of recent advances in an understanding of sex determination.

The haploid condition in animals is characteristic of the gametes. There are no cases of alternating haploid and diploid generations as in plants. But there are two or three types at least in which one sex is diploid and the other haploid. In the Hymenoptera and a few other insects the female is diploid and the male haploid, at least in the early stages of development. In Rotifera the females are diploid and the males are haploid. There is no evidence in either group of sex-chromosomes as such. At present no explanation resting on experimental evidence can be offered to explain these relations. Until such evidence is forthcoming the possible theoretical interpretations that have been suggested are not illuminating.

In *Drosophila* on the other hand where a known sex mechanism is at hand, and where there is experimental evidence bearing on the problem of balance of the genes involved in sex-determination, there is a recent observation by Bridges that is significant. Two mosaic individuals were found which, from genetic evidence, seemed probably to be composites, in part haploid and in part diploid. In one case the haploid region includes the loca-

tion of a secondary sex-organ, the sex-comb (present in the normal male, absent in the female). In the mosaic the sex-comb is absent in the region that is haploid. In other words the haploid group of chromosomes consisting of three autosomes and one X gives, as anticipated, the same kind of result as six autosomes and two X's. The balance is the same in each although the haploid region of the mosaic has only one X, as has the normal male; but in the male this is offset by six autosomes.

The converse case is reported by Wettstein who produced by artificial means gametophyte moss plants that were diploid. If these arise from a haploid female gametophyte cell they are female, and if from a haploid male gametophyte cell they are male. In both cases the balance remains as before. It is apparent that sex determination is not in these cases regulated by the number of the chromosomes but by the relation of contrasted sets of genes or chromosomes to one another.

SEX AND ITS DEFINITION IN LOWER PLANTS

The question of sex terminology appears in its most acute form in the results of recent work on certain groups of gilled fungi or toadstools, Basidiomycetes. In this group, according to a recent statement by Hanna "The problem of sex has occupied the attention of mycologists for more than a hundred years." The discoveries of Miss M. Bensaude (1918), of Kniep (1919-23), of Miss Mounce (1921-22), Buller (1924) and Hanna (1925) have brought to light an extraordinarily interesting situation. In order to simplify the description of this work, the recent paper of Hanna is here followed closely. By means of a new and refined technique, single spores from the gills of the toadstool can be isolated.

From each spore a single mycelium of hyphae can be grown in dung-agar cultures. Each such monosporous mycelium can then be tested by bringing it in contact with the others one by one. Certain of these combinations will unite and form a secondary mycelium on which "clamp connections" develop, indicating that the two mycelia are of "opposite sexes." Later, fruiting bodies or toadstools develop from such mycelia. On the other hand, other combinations when made, do

		AB				ab				Ab		aB	
		51	52	54	55	57	58	59	50	56	53		
AB	51	-	-	-	+	+	+	+	-	-	-		
	52	-	-	-	+	+	+	+	-	-	-		
	54	-	-	-	+	+	+	+	-	-	-		
	55	+	+	+	-	-	-	-	-	-	-		
ab	57	+	+	+	-	-	-	-	-	-	-		
	58	+	+	+	-	-	-	-	-	-	-		
	59	+	+	+	-	-	-	-	-	-	-		
	50	-	-	-	-	-	-	-	-	-	+		
Ab	56	-	-	-	-	-	-	-	-	-	+		
	53	-	-	-	-	-	-	-	+	+	-		

FIG. 10. RECORD OF UNION (+) OR FAILURE (-) BETWEEN MONOSPOROUS MYCELIA OF *COPRINUS LACOPUS* OF SAME PARENTAGE

The mycelia are here classified into four kinds. AB, ab, Ab, aB, according to their behaviour with one another. (After Hanna.)

not form secondary mycelia with clamp connections, and, as a rule, do not produce fruit bodies. The union is interpreted to mean that the mycelia in question are of opposite sex.

Now, when monosporous mycelia from the same strain, (i.e., from plants living in the same locality) are tested, the results are like those in Fig. 10. Here, the presence of clamp connections, formed after the union of two monosporous mycelia, is indicated by the + sign. Failure in this respect is indicated by the —

sign. In the table the mycelia fall into four groups (those belonging to the same group have been brought together in the table). The result is interpreted as meaning that the spores of a single fruit body of the species studied namely *Coprinus lagopus*, belong to four sexual groups.

These four groups as Kniep first showed, can be accounted for on the assumption of two pairs of Mendelian factors that may be designated Aa and Bb. If these factors are segregated, at the time when the

sporous mycelia lie singly in the protoplasm. After union of two mycelia, the nuclei in the derived (secondary) mycelium are in pairs. It is reasonable to assume that one member of each pair has come from one mycelium, the other one from the other mycelium. At the time when the four spores are about to develop, reduction is supposed to take place, so that each spore comes to contain a reduced nucleus. Each spore gives rise to a new reduced mycelium. Such a picture

		A^4B^4	a^4b^4	A^4b^4	a^4B^4
A^2B^2	25	+	+	+	+
	26	+	+	+	+
	27	+	+	+	+
	28	+	+	+	+
a^2b^2	20	+	+	+	+
	23	+	+	+	+
	24	+	+	+	+
a^2B^2	21	+	+	+	+
	29	+	+	+	+
A^2b^2	30	+	+	+	+
	16	+	+	+	+

FIG. 11. RECORDS OF UNIONS BETWEEN UNISPOROUS MYCELIA OF *COPRINUS LAGOPUS* FROM DIFFERENT STRAINS, A⁺ 2⁺ B⁺ b⁺ AND A⁺ 2⁺ B⁺ b⁻.
(After Hanna)

spores are formed on each basidium, there will be present on each toadstool four kinds of spores, AB, ab, Ab, aB, each of which gives rise to a mycelium of the same genetic composition. As shown in figure 10, only those mycelia differing in both factors unite and form clamp connections. This means that there are four sexes, and only those with different sex factors can combine.

There is also a cytological background that accords excellently with these genetic assumptions. The nuclei in the mono-

accords with the reduction process in higher plants and animals and serves to bring these moulds into line with the genetic results that take place when the chromosomes are reduced from diploid to haploid gametes. It is true that, as yet, it has not been shown in *Coprinus* and related species that we are dealing with a diploid-haploid relation, but it seems not improbable that this is the correct interpretation of the facts as far as known. If so, the sorting out of the genetic factors in these toadstools is the

same in principle as that shown by other plants and animals.

The preceding relations hold for strains occurring in any one locality. If strains from different localities are tested, an extraordinary result is found. All the monosporous mycelia of one strain unite (i.e., give mycelia with clamp connections, etc.) with all the monosporous mycelia of the other strains. In figure 11 the pairing of eleven monosporous mycelia from a fruit body from one locality (Edmonton, Canada) are shown to have united with eleven monosporous mycelia from another locality (Winnipeg). The same results were obtained whenever

such hybrid origin will behave in a manner similar to that shown by mycelia from a single source, in that two given mycelia form clamp connections only in case they carry no factors in common.

Here we have the phenomenon of sex exhibited on a grand scale if we interpret the factors involved as sex factors in the conventional sense. There is no objection to using the word in this way if it seems advantageous to define sex on such a basis. Personally, I think it is simpler to interpret the results in the same way as East has interpreted the results of his tobacco investigations, and call the factors involved self-sterility fac-



FIG. 12. SWARMING OF MALE GAMETES AROUND "FEMALE" GAMETE (TO LEFT). UNION OF A "MALE" GAMETE AND A "FEMALE" GAMETE (TO RIGHT)
(After Hartmann)

strains from different localities were paired. The combinations carried out by Hanna gave twenty sexes for *Caprinus* and no doubt the number could be greatly increased by extending the combinations to other localities.

Not only was cross-hybridizing carried out, but the factorial hypothesis was further tested by experiments on the crossed strains themselves. If the factors from the different strains are treated as allelomorphic pairs, and the factors in one strain are designated by Aa and Bb, and those in another strain by A²a² and B²b²; there will be sixteen possible hybrids formed by the union of the mycelia from these two varieties, and each mycelium of

tors (see below). The explanation is the same in principle, whatever language one prefers to use in describing them.

Under the title of Research on Relative Sexuality, Hartmann has recently described results that he obtained with the marine alga, *Ectocarpus siliculosus*. The motile swarm-spores set free from the plants are externally alike, but according to their subsequent behavior they fall into two classes "females" and "males." The former quickly settle down, while the latter continue to swarm for some time and surround the female individual (fig. 12). One of the male swarm-spores finally fuses with the resting female swarm-spore. Hartmann isolated individual parent plants

and when the swarm spores were set free tested these *en masse* against each other. A typical result is given in figure 13 (to the left) where union is indicated by the + sign and failure to unite by the - sign. Each kind is tested against each of the other kinds. In most cases the swarm-spores from a given individual behave constantly either as males or as females with the other types, but in a few instances swarm-spores that acted as females in some combinations acted as males in other combinations. Thus No. 4 (see fig. 13, to left) and No. 13 give results inconsistent with their reaction

tent these relations may be affected by age-factors (settling down, for example), or by environmental factors is not entirely clear, although Hartmann's statement that the relations hold from day to day as the swarm-spores are tested seems to exclude such explanations. Unfortunately the material is not suited to a genetic analysis of the factors involved. Whether the quicker settling down of gametes from a certain individual is a sufficient index of their "sex" and if so, how this is changed when a weak female acts as a male, etc., is not apparent. Nevertheless the failure of gametes from

	3♂	4♀	5♀	7♀	11♂	13♀	14♀
3♂	—	+	+	+	—	+	+
4♀	+	—	—	—	+	+	—
5♀	+	—	—	—	+	—	—
7♀	+	—	—	—	—	+	—
11♂	—	+	+	—	—	+	—
13♀	+	+	—	+	+	—	+
14♀	+	—	—	—	—	+	—

	31♀	32♀	33♂	35♂	38♂	40♂
31♀	—	—	+	+	+	+
32♀	—	—	+	+	+	+
33♂	+	+	—	+	—	—
35♂	+	+	+	—	+	—
38♂	+	+	—	+	—	—
40♂	+	+	—	—	—	—

FIG. 13. RECORD OF UNION (+) OR FAILURE (—) TO UNITE BETWEEN THE GAMETES FROM DIFFERENT PLANTS (ECTOCARPUS)
(After Hartmann)

in other combinations. Another exception is found in the reactions between No. 35 and No. 38 (see fig. 13, to right), both of which are designated as males from their general behaviour, yet react to each other as male and female. Hartmann speaks of certain individuals as strong males, others as weak males, certain individuals as strong females and others as weak females according to the numbers of "clusters" that they give in different combinations, and concludes that weak females may function as males when opposed to strong females, and that weak males may function as females when opposed to strong males. To what ex-

the same plant to copulate appears to put the phenomenon in the same category as self-sterility present in other groups. Whether self-sterility and its correlative cross-fertility is to be taken as a criterion of sex is perhaps largely a matter of choice or of definition at present. Personally it seems to me to confuse rather than clear up the problems involved to use the word sex in this connection where the phenomenon is rather one of union of gametes or their failure to unite—due possibly to self-sterility factors—than one of sex as commonly understood.

The question may be seriously asked whether it may not be simpler and less

likely to lead to confusion to call the factors involved in the union of the mycelia of *Coprinus* and of the swarm-spores of *Ectocarpus*, self-sterility factors rather than sex-factors. The recent brilliant results of East in his studies on self-sterility in tobacco have for the first time put the oft-studied problem of cross- and self-fertility in flowering plants on a well tested genetic basis. These phenomena in the flowering plants have many resemblances to the union of the gametes in *Coprinus* and *Ectocarpus* and while the *modus operandi* of the process may not be identical in all cases there is much to suggest that the genetic and physiological backgrounds may be essentially alike.

In the brief paper of East and Mangelsdorf is given a summary of work extending over several years dealing with the inheritance of self-sterility in crosses between two species of tobacco, viz. *Nicotiana glauca* and *N. glauca*. Only the most general conclusions can be given here. By special manipulation several selfed, homozygous strains of self-sterile individuals were carried through twelve generations to obtain suitable material for testing the problem. As an example the results of one type of the resulting families may be given. Three kinds of individuals a, b and c were found. Each individual of any one of these kinds is sterile with any other individual of the same class and fertile with each individual of the other two kinds; but the progeny resulting from reciprocal crosses is different. Thus, a ♀ by c ♂ gives b and c individuals only, while c ♀ by a ♂ gives only a and b individuals. Two classes always appear in equal numbers, but the class of the mother is never represented in the offspring. The explanation is as follows. If three allelomorphous genes are present in such a family $S_1 S_2 S_3$

and if class a = $S_1 S_3$; class b $S_1 S_2$; class c $S_2 S_3$ and if the pistil of a plant affords the stimulus for the growth of the pollen which bears sterility factors other than its own, the results find a consistent explanation. For instance, plant c ($S_2 S_3$) affords a sufficient stimulus only to pollen carrying factors other than $S_2 S_3$. Only pollen bearing the factor S_1 can penetrate the style and fertilize the eggs. The progeny will be $S_1 S_2$ (class b) and $S_1 S_3$ (class a) in equal numbers. Reciprocally, a ♀ ($S_1 S_2$) by c ♂ ($S_2 S_3$) permits the S_2 pollen alone to penetrate to the eggs giving $S_1 S_2$ (b) and $S_2 S_3$ (c). This result which is typical of all the others, explains why the female combination is absent in the progeny, why the progeny of reciprocal crosses is different and why the progeny-counts of two classes other than the female are equal regardless of which of the other two classes serves as the male parent.

There are several ways of testing the validity of this hypothesis. The tests have been made and the hypothesis confirmed. This convincing analysis, the result of carefully planned genetic experiments, is a contribution of the first rank to a problem that has baffled students of fertilization for seventy-five years and more. The solution is not only a keen genetic analysis of the case but gives an insight into the physiological reactions between the haploid pollen tube and the diploid tissue of the female. It has been shown by direct observation that the rate of growth of the pollen tube in the tissue of the female is consistent with the view that a differential rate of growth is actually present. The nature of the relation is not known at present but may reasonably be assumed to be chemical in nature. It is possible that the same or a similar chemical reaction with its genetic basis may account for the

self-sterility observed in the union of genetically unlike mycelia of lower forms. If this can be established the genetic problem has to deal primarily with self-sterility factors that are probably Mendelian genes. It may seem of doubtful value to identify these factors with sex factors which conventionally at least apply rather to somatic differences in dioecious types or to those with separate sexes. It is true that amongst these differences are those concerned with producing eggs and sperm whose main function is to unite with each other, but, as generally understood, these functions are less conspicuous than those appertaining to the bodily constitution of male and female individuals.

GENES IN THE Y-CHROMOSOME

Earlier work on the sex-cells of those insects that have an unequal pair of sex-chromosomes in the male had shown that the smaller member (Y) of the pair is confined to the male line. In different species all degrees of inequality between X and Y were soon discovered, and in a few cases no Y at all was found, leaving the X as an unpaired chromosome in the male. Since in the last case it was obvious that a Y-chromosome is unnecessary for the production of a normal male, the variation in size of the Y in different species gave the impression that the Y-chromosome had less significance in sex determination than the X-chromosome, and might even be lost without any change in the mechanism. The female would thus be due to the presence of two X's and the male to the presence of one X-chromosome.

This implication resting on cytological findings seemed to be confirmed by the discovery that the Y-chromosome of *Drosophila melanogaster* does not carry a set of genes comparable to those found in

the other chromosomes, or more accurately stated, the inheritance of characters whose genes are carried by the X-chromosomes may be treated as though the Y-chromosome carries no genes that are dominant to them; in other words, that the Y-chromosome may generally be ignored or treated as though it were "empty." Taken literally the last statement seemed absurd and has furnished some of the critics of the chromosome mechanism with material for ridicule. These critics have generally overlooked the fact that the above statements about the Y-chromosome are no more than a conclusion from genetic evidence which they would scarcely dispute. They overlooked also the fact that the workers in *Drosophila* have been careful to state, more than once, that their results do not show the Y-chromosome to be empty except in the sense that it contains no genes that have as yet been found to behave as dominants to recessive genes of the X-chromosome. Moreover, it is sometimes forgotten that a male *Drosophila* without a Y-chromosome is sterile although in all other respects his characters are normal. It has further been shown that the presence of a Y or even two Y's in the female (which is occasionally brought about by its transfer from the male line) does not affect the female characters in any visible degree. Its presence causes irregularities in the distribution of the sex-chromosome at the maturation division, in the same way as does an unpaired chromosome of any other pair, but this concerns rather the mechanism of reduction, and does not relate to the genic composition of the Y-chromosome itself. Until evidence is brought forward that the Y-chromosome of *D. melanogaster* carries genes that must be reckoned with in the study of inheritance, the facts enumerated above may stand.

Some recent discoveries, furnishing genetic evidence that the Y-chromosome in other animals carries genes comparable to the genes in other chromosomes and that the genes cross over with those in the X, have been hailed with delight by the opponents of the chromosome theory as evidence that the conclusions concerning the Y-chromosome in *Drosophila* are

that no crossing-over takes place between these parts. The following diagram (fig. 14) will serve to illustrate how this mechanism gives the same kind of result, so far as sex is concerned, as does the occurrence of independent sex-chromosomes. There is involved, however, another set of problems relating to sex-linked inheritance.

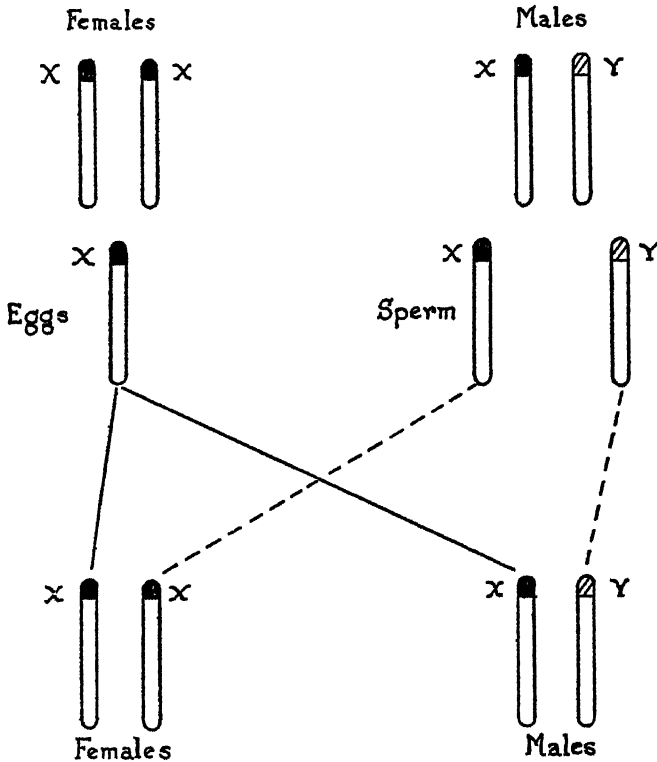


FIG. 14. DIAGRAM OF SEX-CHROMOSOMES, X (BLACK) AND Y (CROSS-LINED) UNITED TO AUTOSOMES

If there is no crossing over between the X- and the Y-component in the male, the Y-chromosome remains in the male line.

in some way compromised. There is, however, a probable solution that involves a familiar cytological conclusion, namely, that the sex-chromosomes may be a part of, or have become attached to, a pair of autosomes. This means no more than that one part only of the "sex-chromosomes" has the function of an X- or Y-chromosome, which means again that the Y-part is different from the X-part, and

If no crossing-over takes place between X- and Y-components, but may take place between the autosomal parts of this pair, the inheritance of characters whose genes are carried in the autosomal parts will be expected to show partial linkage to sex and to the characters whose genes lie in the X-component. It is not necessary to point out here the details of this sort of inheritance, but it may be stated

that it will be consistent with the facts so far reported for cases where the "Y" is said to carry genes that interchange with those of the "X." A few facts recently obtained may be cited.

confirmed by Winge, that when the male of one race is bred to a female of another race the sons are colored like the father. If these hybrids are inbred, the sons are again like the father, i.e., they have not

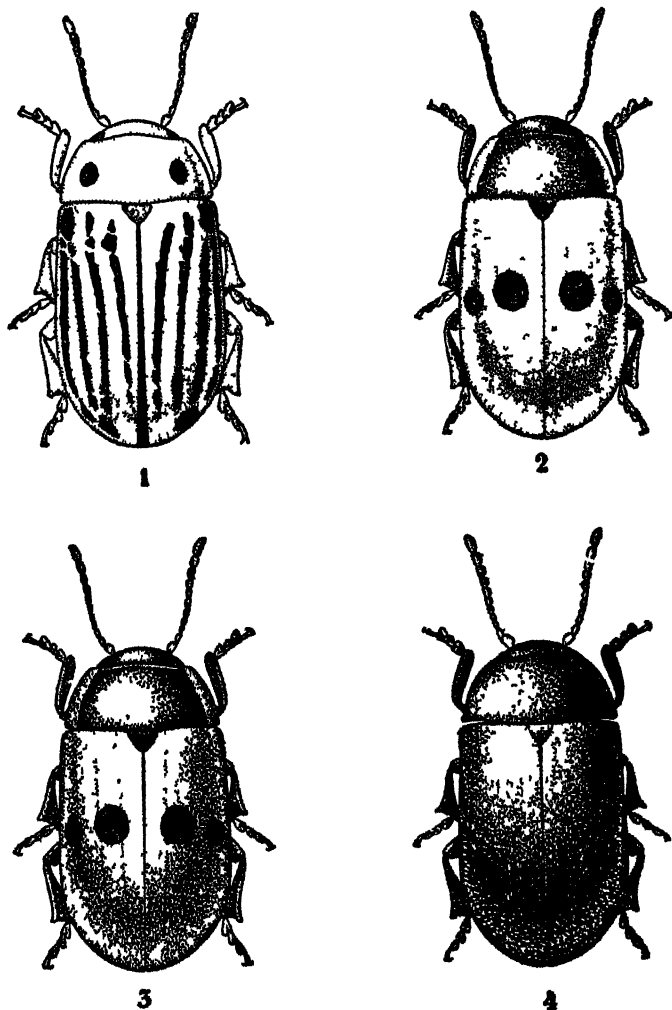


FIG 15 FOUR TYPES OF THE BEETLE, *PHYTODECTA VARIABILIS*, NAMELY, 1, DE LINEAS, 2, AMARILLO, 3, ROJO, 4, NEGRO
(After Zulueta)

In the aquarium fish, *Lebistes reticulatus*, the females of different races are closely similar in coloration while the males are differently marked. It was shown first by Schmidt (1920) and later

inherited any color through the mother. The same relation appears in later generations and in all combinations tested. A similar type of inheritance was independently discovered by Aida in another

fish, *Aplocheilus*, inhabiting the paddy fields of Japan. The results are explicable on the view that the genes for the different kinds of colors are carried both by the X- and by the Y-chromosome.

A further fact of importance was reported by Winge and by Aida. There may take place an interchange between the "X" and the "Y" in the male, or at least certain results can only be explained on the assumption that occasionally such an interchange takes place. As stated above this result also can be brought into line with the sex-chromosome formula, provided the interchange

The experiments show that type de líneas (L) is recessive to any of the others, that amarillo (A) is in turn recessive to the other two, that rojo (R) is recessive to negro (N). The order of dominance is $L < A < R < N$. Treating these as allelomorphic, only two of the same kind, or one only of each of two kinds can be present in the same individual at the same time. A further fact also emerges, namely, that the genetic results can be explained only on the assumption that the chromosomes that carry these genes are the sex-chromosomes. This means that any one of the genes may be

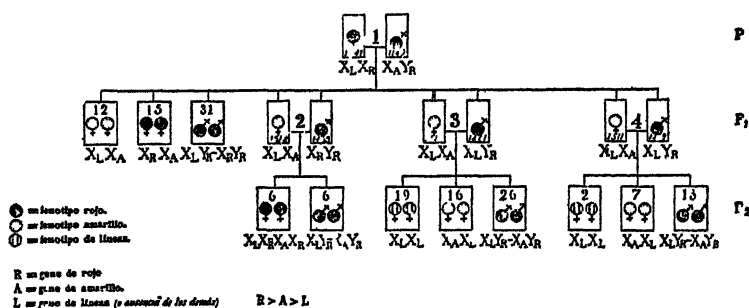


FIG. 16. PEDIGREE OF A CROSS BETWEEN TYPES, ROJO, FEMALE (SEE FIG. 15), HETEROZYGOUS FOR DE LÍNEAS AND TYPE ROJO, MALE, HETEROZYGOUS FOR AMARILLO

The Y-chromosome is here represented as carrying a gene for rojo, and the X-chromosome as carrying the allelomorphic gene. (After Zulueta.)

takes place only between the autosomal components of the chromosomes in question.

A remarkable case of transmission through the "Y" has recently been described by Zulueta for a Spanish beetle, *Phytodecta variabilis*. As shown in figure 15 there are four distinct color types of these beetles that are called by Zulueta (1) de líneas, or striped, (2) amarillo, or yellow, (3) rojo, or red, and (4) negro, or black. Crossing experiments with these types show that any one of them behaves towards any other one as an allelomorph. In other words, the genetic results can be treated as a case of multiple allelomorphism.

present in the X's, and any one in the Y of the male line. The sex formula is $XX-XY$.

The experiment illustrated in the diagram (fig. 16) gives the results of a cross in which a female rojo, heterozygous for de líneas ($X_L X_R$) is mated to a male rojo heterozygous for amarillo ($X_A Y_R$). The offspring (F_1) are of two kinds, and this is consistent with the formula employed. Certain of the F_1 's were mated to each other to give an F_2 generation. Here three types appear which again are expected. Other matings give the same kinds of results, all of which can be interpreted as above, on the assumption that the Y-chromosome may carry any one of the four genes.

If these genes are in the sex-components which, *ex hypothesi*, do not interchange, the question arises as to how the same kinds of allelomorphs may be present in the X- as well as in the Y-component. One answer would be that they have arisen from the same kind of original gene as independent mutations, sometimes in the X-component, sometimes in the Y-component. There are, in fact, some curious facts relating to the distribution of the males in different districts,—facts that are perhaps consistent with the above assumption of independent mutation in X and Y. In some districts certain mutant types of males are absent while in other districts these types are abundant. This is consistent with the assumption of independent mutation in the two chromosomes, but another explanation

will do as well. Suppose, for instance, that the genes for the four color markings are not present in the X- and Y-components but in the autosomal components and that they are allelomorphs. The results will then be explicable on the assumption that there is either no crossing-over in the male or that it is so infrequent as not to have arisen in Zulueta's experiments. If, however, it should take place on rare occasions in the male between the autosomal components, the facts relating to the distribution of the different kinds of males may be accounted for. Hence on either view, that of independent mutation in the sex-chromosomes, or that of rare crossing-over in the male in the autosomal component, the facts as far as known can be explained.

LIST OF LITERATURE

- ALLEN, C. E. 1917. A chromosome difference correlated with sex differences in *Sphaerocarpos*. Science, N.S., xlii.
- . 1919. The basis of sex inheritance in *Sphaerocarpos*. Proc. Am. Philos. Soc., lvi.
- BAUR, E. 1912. Ein Fall von geschlechtbegrenzter Vererbung bei *Melandrium album*. Zeit. Abst.-Vererb., viii.
- BĚLAŠ, K. 1924. Neue Untersuchungen über Geschlechtschromosomen bei Pflanzen. Zeit. Abst.-Vererb., xxxv.
- BENSAUDE, M. 1918. Recherches sur le cycle évolutif et la sexualité chez les Basidiomycetes. Nemours.
- BLACKBURN, K. B. 1923. Sex chromosomes in plants. Nature, cxii.
- . 1924. The cytological aspects of the determination of sex in the dioecious forms of *Lychnis*. Brit. Jour. Exp. Biol., i.
- BLACKBURN, K. B. AND HARRISON, J. W. H. 1922. The meiotic phase in the Salicaceae. Report Brit. Assoc. Adv. Sc., p. 298.
- . 1924. Genetical and cytological studies in hybrid roses. Brit. Jour. Exp. Biol., i.
- . 1924. A preliminary account of the chromosomes and chromosome behavior in the Salicaceae. Ann. Bot., xxxviii.
- BLIKER, H. 1925. Chromosomenstudien bei der Gattung *Trifolium*. Jahrb. wiss. Bot., lxiv.
- BRAUN, H. 1909. Die spezifischen Chromosomenzahlen der einheimischen Arten der Gattung *Cyclops*. Arch. f. Zellf., iii.
- BRIDGES, C. B. 1916. Non-disjunction as proof of the chromosome theory of heredity. Genetics, i.
- . 1921. Genetical and cytological proof of non-disjunction of the fourth chromosome of *Drosophila melanogaster*. Proc. Nat. Acad. Sc., vii.
- . 1922. The origin of variations in sexual and sex-limited characters. Am. Nat., lvi.
- . 1925. Haploidy in *Drosophila melanogaster*. Proc. Nat. Acad. Sc., xi.
- BULLER, A. H. R. 1924. Experiments on sex in mushrooms and toadstools. Nature, cxiv.
- CLAUSEN, R. E. AND GOODSPED, T. H. 1925. Inter-specific hybridization in *Nicotiana*. II. A tetraploid *glutinosa-tabacum* hybrid, an experimental verification of Winge's hypothesis. Genetics, x.
- COLLINS, J. L. AND MANN, M. C. 1923. Inter-specific hybrids in *Crepis*. II. A preliminary report on the results of hybridizing *Crepis setosa* Hall with *C. capillaris* (L.) Wallr. and with *C. biennis* L. Genetics, viii.
- DELAUNAY, L. 1915. Etude comparée caryologique de quelques espèces du genre *Muscaria* Mill. Mem. Soc. Nat., Kiev. (Russian).

- DELAUNAY, L. 1922. Comparative caryological study of species of *Muscari* and *Bellevalia*. Review of the Tiflis Bot. Garden, Series II, No. 1. (Russian.)
- . 1925. The S-chromosomes in *Ornithogalum* L. Science, lxii.
- DIGBY, L. 1912. The cytology of *Primula hawensis* and of other related *Primula* hybrids. Ann. Bot., xxxvi.
- EAST, E. M. AND MANGELSDORF, A. J. 1925. A new interpretation of the hereditary behavior of self-sterile plants. Proc. Nat. Acad. Sc., xi.
- EMERSON, R. A. 1924. A genetic view of sex expression in the flowering plants. Science, lix.
- ERNST, A. 1918. Bastardierung als Ursache der Apogamie im Pflanzenreiche. Jena.
- GOODSPEED, T. H. 1923. A preliminary note on the cytology of *Nicotiana* species and hybrids. Svensk. Bot. Tidskr., xvii.
- HANNA, W. F. 1925. The problem of sex in *Coprinus lagopus*. Ann. of Bot., xxxix.
- HARRISON, J. W. H. AND PRACOCK, A. D. 1925. On Parthenogenesis originating in Lepidopterous crosses. Trans. Nat. Hist. Soc. of Northumberland, Durham, and Newcastle-upon-Tyne, New series, vi.
- HARTMANN, M. 1923. Über sexuelle Differenzierung und relative Sexualität. Studia Mendeliana, Brünn.
- . 1925. Untersuchungen über relative Sexualität. I. Versuche an *Ectocarpus siliculosus*. Biol. Zentr., xlv.
- HEILBORN, O. 1922. Die Chromosomenzahlen der Gattung *Carex*. Svensk Bot. Tidskr., xvi.
- HIRATA, K. 1924. Sex reversal in hemp. (Preliminary report.) Jour. Soc. Agric. and Forestry, xvi.
- KARPETSCHENKO, G. D. 1925. Karyologische Studien über die Gattung *Trifolium* L. Bull. Applied Bot. and Plant Breeding, xiv.
- KIHARA, H. AND ONO, T. 1923. Cytological studies on *Rumex* L. I. Chromosomes of *Rumex acetosa* L. Bot. Mag. Tokyo, xxxvii.
- . 1923. Cytological studies on *Rumex* L. II. On the relation of chromosome number and sexes in *Rumex acetosa* L. Ibid., xxxvii.
- . 1925. The sex-chromosomes of *Rumex acetosa*. Zeit. Abst.-Vererb., xxxix.
- KNEIP, H. 1919. Über morphologische und physiologische Geschlechtsdifferenzierung. Verhandl. der Physikal.-Med. Gesell. zu Würzburg.
- . 1922. Über Geschlechtsbestimmung und Reduktionsteilung. Ibid., xlvii.
- . 1923. Über erbliche Änderungen von Geschlechtstaktoren bei Pilzen. Zeit. f. induk. Abst.-Vererb., xxxi.
- KOJIMA, H. 1925. On the meiosis and the chromosome number in different races of *Solanum Melongena* L. Bot. Mag. Tokyo, xxxix.
- LJUNGDAHL, H. 1922. Zur Zytologie der Gattung *Papaver*. Vorl. Mitt. Svensk Bot. Tidskr., xvi.
- . 1924. Über die Herkunft der in der meiosis konjugierenden Chromosomen bei *Papaver*-Hybriden. Svensk Bot. Tidskr., xviii.
- MANN, M. C. 1925. Chromosome number and individuality in the genus *Crepis*. I. A comparative study of the chromosome number and dimensions of nineteen species. Univ. Calif. Pub. Agri. Sc., ii.
- MARCHAL, E. 1920. Recherches sur les variations numérique des chromosomes dans la série végétale. Mémoires de l'Académie royale de Belgique ser. 2, ii.
- MCPHER, H. C. 1924. Meiotic cytogenesis of *Cannabis*. Bot. Gaz., lxxviii.
- MEYER, C. W. AND MOSES, M. S. 1923. Chromosomes of *Drosophila*. Chromosome relationships and genetic behavior in the genus *Drosophila*: I. A comparison of the chromosomes of different species of *Drosophila*. Jour. Hered., xiv.
- MEURMAN, O. 1925. Über Chromosomenzahlen und Heterochromosomen bei diözischen Phanerogamen. Vorl. Mitt. Societas Scientiarum Fennica. Comment. Biologicae, ii, 2.
- . 1925. The chromosome behavior of some dioecious plants and their relatives with special reference to the sex chromosomes. Ibid., ii, 3.
- MEYER, P. 1923. Crossing-over und Chromosomen. Ein Beitrag zur Frage des Faktorenaustauschmechanismus. Zeit. Abst.-Vererb., xxxii.
- MORGAN, L. V. 1925. Polyploidy in *Drosophila melanogaster* with two attached X chromosomes. Genetics, x.
- MORGAN, T. H. 1922. Croonian lecture On the mechanism of heredity. Proc. Roy. Soc., xciv.
- . 1926. The theory of the gene. Yale Univ. Press.
- MORGAN, T. H., BRIDGES, C. B. AND STURTEVANT, A. H. 1925. The Genetics of *Drosophila*. Bibliographia Genetica, ii.
- MOUNCH, I. 1921. Homothallism and the production of fruit-bodies by monosporous mycelia in the genus *Coprinus*. Trans. Brit. Mycolog. Soc., vii.
- . 1922. Homothallism and heterothallism in the genus *Coprinus*. Ibid., viii.
- NAWASCHIN, S. 1912. On the dimorphism of the nuclei in the somatic cells of *Galtonia candida*. Bull. Acad. Imper. Sc. Petersburg, xxii. (Russian.)

- NAWASCHIN, S. 1915. Hetero- and idiochromosomes of the plant's nucleus as the cause of the nuclear dimorphism of certain plant species, and the significance of nuclear dimorphism in the process of the origin of the species. *Ibid.*
- PELLEW, C. AND DURHAM, F. M. 1916. The genetic behavior of the hybrid *Primula kewensis*, and of its allies. *Jour. Genet.*, v.
- ROSENBERG, O. 1918. Chromosomenzahlen und Chromosomendimensionen in der Gattung *Crepis*. *Arch. f. Bot.*, xv.
- . 1920. Weitere Untersuchungen über die Chromosomenverhältnisse in *Crepis*. *Svensk Bot. Tidskr.*, xiv.
- SANTOS, J. K. 1923. Differentiation among chromosomes in *Elodea*. *Bot. Gaz.*, lxxv.
- . 1924. Determination of sex in *Elodea*. *Ibid.*, lxxvii.
- SCHACKE, M. A. 1919. A chromosome difference between the sexes of *Sphaerocarpus texanus*. *Science*, N.S., xlix.
- SCHMIDT, JOHNS. 1920. The genetic behaviour of a secondary sexual character. *C. R. Trav. Labor. Carlsberg*, xiv.
- SEILER, J. 1914. Das Verhalten der Geschlechtschromosomen bei Lepidopteren. *Arch. f. Zellf.*, xiii.
- . 1917. Geschlechtschromosomenuntersuchungen an Psychiden. *Zeit. Abst. Vererb.*, xviii.
- SHIMOTOMAI, N. 1925. A karyological study of *Brassica* I. *Bot. Mag. Tokyo*, xxxix.
- SHULL, G. H. 1910. Inheritance of sex in *Lychnis*. *Bot. Gaz.*, xlix.
- . 1911. Reversible sex-mutants in *Lychnis dioica*. *Ibid.*, lii.
- . 1914. Sex-limited inheritance in *Lychnis dioica* L. *Zeit. Abst. Vererb.*, xii.
- SINOTO, Y. 1924. On the chromosome behaviour and sex determination in *Rumex acetosa* L. *Bot. Mag. Tokyo*, xxxviii.
- SOROKINS, HELEN. 1924. The satellites of the somatic mitoses in *Ranunculus acris* L. *Pub. Fac. Sc. Univ. Charles, Prague*.
- STEVENS, N. M. 1905. Studies in spermatogenesis with especial reference to the accessory chromosome. *Carnegie Institution Wash. Pub.*, xxxvi.
- TÄCKHOLM, G. 1922. Zytologische Studien über die Gattung *Rosa*. *Acta Hort. Berg.*, vii.
- TAKARA, M. 1910. Über die Zahl der Chromosomen von *Crepis japonica*. *Bot. Mag. Tokyo*, xxiv.
- . 1921. Cytologische Studien an Einigen Kompositen. *Jour. Coll. Sc. Tokyo Imp. Univ.*, xliii.
- TISCHLER, G. 1915. Chromosomenzahl—Form und—Individualität im Pflanzenreich. *Progr. Rei Bot.*, v.
- VANDENDRIES, R. 1923. Recherches sur le déterminisme sexuel des Basidiomycètes. *Bruxelles*.
- . 1923. Nouvelles recherches sur la sexualité des Basidiomycètes. *Bull. d. l. Soc. Royale d. Bot. d. Belgique*, xvi.
- WETSTEIN, F. V. 1924. Über Fragen der Geschlechtsbestimmung bei Pflanzen. *Die Naturwissenschaften*, xii.
- WILSON, E. B. 1905. Studies on chromosomes. I. The behavior of the idiochromosomes in Hemiptera. *Jour. Exp. Zool.*, ii.
- . 1909. Studies on chromosomes. IV. The "accessory" chromosomes in *Syromastes* and *Pyrrhocoris*, with comparative review of the types of sexual differences of the chromosome groups. *Ibid.*, vi.
- WINGE, Ö. 1914. The pollination and fertilization processes in *Humulus lupulus* L. and *H. japonicus* Sieb. et Zucc. *C. R. Trav. Labor. Carlsberg*, xi.
- . 1917. The chromosomes. Their numbers and general importance. *Ibid.*, xiii.
- . 1922. One-sided masculine and sex-linked inheritance in *Lebistes reticulatus*. *Jour. Genet.*, xii.
- . 1923. Crossing-over between the X- and the Y-chromosome in *Lebistes*. *Ibid.*, xiii.
- . 1923. On sex chromosomes, sex determination and preponderance of females in some dioecious plants. *C. R. Trav. Labor. Carlsberg*, xv.
- WINKLER, H. 1916. Über die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. *Zeit. Bot.*, viii.
- . 1920. Verbreitung und Ursache der Parthenogenesis im Pflanzen- und Tierreiche. *Jena*.
- YAMPOLSKY, C. 1919. Inheritance of sex in *Mercurialis annua*. *Am. Jour. Bot.*, vi.
- DE ZULUETA, A. 1925. La herencia ligada al sexo en el coleóptero *Phytodecta variabilis* (Ol.) "Eos" i.



THE ANTIQUITY AND DISPERSAL OF VASCULAR PLANTS

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AGE AND AREA

A DECADE ago (79, p. 325), after compiling and studying statistics covering the endemic vascular plants of Ceylon, Dr. J. C. Willis put forward his "law" of Age and Area; and a year later he had so far progressed in his studies as to state that "The law which appears to me to govern the distribution of species may be thus tentatively expressed: 'the area occupied by any given species (taken in groups of twenty or so) at any given time in any given country in which there occur no well-marked barriers depends upon the age of that species in that country'" (81, p. 438). Extending his statistical studies to the Angiosperms and sometimes to the Pteridophytes of New Zealand, Brazil and other areas, including oceanic islands and the British Isles, Willis continued to amass a body of summaries and generalizations and to enunciate corollaries at a rate quite dazzling to others.

The original proposition, reduced to its simplest terms, might well be stated: given a static world the longer a plant (or animal) lives the more opportunity it will have to spread; consequently, the older a species the wider its range. But at once Willis was challenged by close students of various floras, who pointed out that, although the primary "law" (which Willis later more modestly referred to as his "hypothesis" and sub-

sequently (91, p. 246) as "simply a corollary") is axiomatic, the world, as a matter of fact, has been anything but static and that the present ranges of plants and animals are due to such a complex of historic and edaphic factors that their ages cannot safely be deduced by studying simply the extent of their present distribution. Many other objections were brought forward by students of floras or faunas, chiefly of England, India, South Africa and North America; while by the mutationists Willis was vigorously applauded.

So long as the discussions were confined to a few journals, and principally to *Annals of Botany*, they were seen by only a limited number of students, but in 1922 Dr. Willis drew together in modified form his chief arguments, and had them supplemented by chapters contributed by some of his supporters, in a handy volume (91) now familiar or readily accessible to all. During the discussions which had followed the publication by Willis of his many deductions his definition of Age and Area greatly altered, a change clearly brought out in the statement by Gleason:

Originally it was, in essence at least, "The area of a species depends on its age;" but now, since one exception after another has been added, it reads:

"The area occupied at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such

as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man, and by other causes."

One can count in this expression of the theorem no less than nine distinct exceptions definitely stated, relating conditions under which the age-and-area principle may not hold. Then, to guard against other criticisms which may arise in the future and which Willis was unable to foresee, he has added the blanket exception "other causes." Lastly, to make his theorem still more nearly impregnable, he has forbidden us to argue against it by citing individual exceptions. In other words, the area of a species depends on its age when it does depend on it, and cases in which it does not must not be mentioned (39, p. 542).

Very frankly, I had supposed that Willis, by piling up so many exceptions in his definition and by shifting at will the magic number of test-cases which one must use, sometimes twenty, sometimes fifteen, sometimes ten, had proved Age and Area a dead issue; and I thought that such students as Bateson (4), Berry (5, 7), Calvert (13), Regan (62), Ridley (65, 66), Schonland (69), Seward (70), and Sinnott (71, 72, 73), had seen it officially buried. But the facts, that in 1923 I was urged to take part in a symposium upon the subject and that I am now again invited to act as medical examiner and coroner, indicate that to those who are not specially in touch with the problems of classification and distribution the hypothesis seems still alive and to make a strong appeal. This is quite natural, for we all take an interest in the larger generalizations in biology and Age and Area is a large generalization. I must, however, make it quite clear that, in a limited discussion I necessarily confine myself chiefly to the few aspects of the question with which I am most familiar and, since Willis, himself, enumerates and discusses many of the objections which have been raised and since they have been clearly discussed by the scores

of careful thinkers referred to in my bibliography, I must refrain from entering at this time into many of these matters.

In some instances I do not understand what Willis means, but I take comfort in the fact that I am not alone. He repeatedly complains that others do not have "a proper understanding of Age and Area, and of the provisos with which it is hedged around" (91, p. 84); Lloyd Praeger, than whom there are few if any keener students of plant geography in Great Britain and Ireland, says: "to be candid, I find it difficult to follow and doubt if I understand it fully. . . . Recently . . . I had the advantage of discussing the theory with its author; but . . . I failed to obtain a clearer understanding. Like the Persian philosopher, I came out by the same door as in I went" (61, p. 122). Bateson characterized the book, *Age and Area*, as "very difficult reading" (4, p. 43) and Berry speaks of Willis's ideas as "embalmed in a very complicated style" (7, p. 547).

The introductory chapters are on the whole really fine and, as Bateson said, clearly demonstrate that Willis actually knows that the world is *not* static. Praeger, too, finds these chapters sane and sound, forming an excellent modern introduction to a general study of phytogeography. But one must wonder at many of the illustrations used and some of the statements of fact. Willis claims not to believe in *adaptations* and in his arguments that they are rarely found in fruits he is very catholic, for he includes among the "genera with little or no mechanism for dispersal" (91, p. 21) the tick trefoils (*Desmodium* or *Mesbomia*), the fruits of which are unwillingly transported by every passing animal. And, in arguing that the largest families of plants (excepting *Compositae* and *Orchidaceae*) "are not remarkable for the posses-

sion of extra good methods of dispersal" (91, p. 21), he enumerates among the examples Milkweeds, *Asclepiadaceae* (which are characterized by having thin and flat seeds with a long coma), the Heaths, *Ericaceae* (many with berries or with fine seeds suggesting those of orchids), Grasses (which he elsewhere admits "to some degree suited to wind dispersal"), the *Rosaceae* (many with fleshy fruits, fine seeds or plumose or bristly fruits), the *Coniferae* (mostly with winged seeds) and the Figworts, *Scrophulariaceae* (chiefly with fine or thin seeds). If these and many others enumerated by Willis appeal to him as lacking adaptations for dispersal, it would seem that he sees adaptations only in bizarre modifications.

RATE OF MIGRATION OF PLANTS

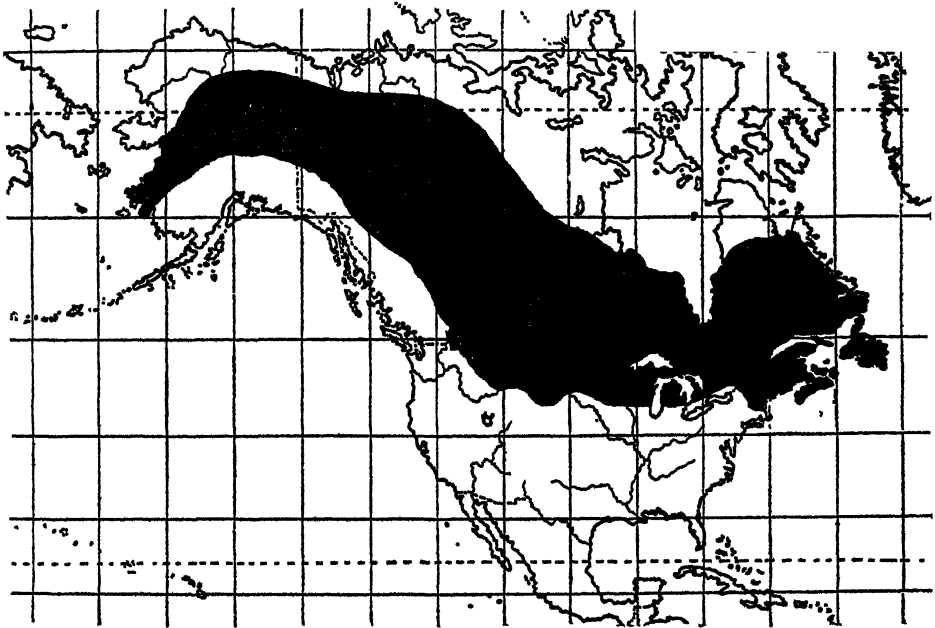
In these introductory chapters Willis makes much of the well known slow rate of migration of most plants and rightly contends, what any ecologist or other student of vegetation in the mass will approve, that in studying distribution whole associations must be taken into account, since the different species move together and are so closely inter-related that an outsider would find it difficult to gain a foothold within the association. As plants with power of specially rapid spread he cites (following Ridley) those with light powder-like seeds or spores as most rapidly spread, those with plumed seeds (dandelion, etc.) next and those with winged seeds (ash, maple, pine, etc.) "the slowest" of those with special mechanisms for dispersal; while plants with seeds like those of bur-reeds (*Sparganium*), *Iris*, *Corydalis*, peas (*Lathyrus*, etc.), touch-me-not (*Impatiens*), violets (*Viola*) and buckbean (*Menyanthes*), solid, rounded and heavy, without plumes or wings, would pre-

sumably be classed as completely handicapped. He cites the *Dipterocarps*, "tall trees with . . . fruit, upon which . . . grow large wings," as fairly rapid travelers, but even in these "a little calculation will show that in the most favorable circumstances conceivable, with the ground clear of other vegetation, it would take about 60,000 years to migrate 100 miles. *Dipterocarpus grandiflorus* . . . ranges from the Malay Peninsula to the Philippines, and Ridley estimates that at least 1½ million years would be needed to traverse this distance" (given continuous land, of course). The distance from the Malay Peninsula to the Philippines is 1000 miles. If specially favored plants with an absolutely clear field would require 1½ million years to cover this distance, what shall we say of the vast Canadian and Hudsonian flora of cool-temperate North America?

This great group of plants of all habitats (coniferous or mixed forest, bog, cliff, rock-barren, sand-hill, stream, lake, meadow, etc.) must, we agree with Willis, be considered as moving *in toto*, not as individual species. Yet this great body of plants, occupying about one-fourth of the area of North America, could not invade the Canadian and Hudsonian 'country from the South until the receding from it of the last Pleistocene ice. In other words, the plants had before them the absolutely clear field required for the hypothetical migration of the wind-dispersed *Dipterocarp*, which, according to Willis, would require 1½ million years to cover 1000 miles. Very conservatively, geologists set 25,000 years ago as the time when the southern edge of the Wisconsin ice began to recede and, of course, a later date when it left the North, very much later since "The time occupied by the recession from

Hartford [Connecticut] to St. Johnsbury [Vermont, a distance of 190 miles] was about 4100 years" (2, p. 74). Yet, as clearly shown in the excellent little maps published by Hough (48), the trees of the Canadian forest have occupied an area varying in length (east to west) from 3800 (practically 4000) miles (White Spruce, *Picea canadensis*—map 1, Balsam Poplar, *Populus balsamifera*, Canoe Birch, *Betula papyrifera*, etc.) to a general minimum of 2000 miles (Red Pine, *Pinus*

Iris (*I. versicolor*), Pale Corydalis (*C. sempervirens*), vetchlings (*Lathyrus palustris*, *ochroleucus*, etc.), touch-me-nots (*Impatiens pallida* and *biflora*), violets (*Viola pallens*, etc.), buckbean (*Menyanthes trifoliata*) and the thousands of other species, both vascular and cellular, which make up the aggregate flora of the Canadian Zone. Obviously, this great Canadian flora covering a region, one-fourth of North America, which was available to plants only within thousands, rather



MAP 1. RANGE OF WHITE SPRUCE, *PICEA CANADENSIS*, AFTER HOUGH (48)

resinosa, White Cedar, *Thuja occidentalis*, American Mountain Ash, *Sorbus americana*, Mountain Maple, *Acer spicatum*, etc.). North and south, within the area of the latest glaciation, the belt is 500 to 1200 miles across. And, occupying the same extremely youthful area with the trees, which have winged fruits, plumose seeds, fleshy fruits or nuts, we find bur-reeds (*Sparganium angustifolium*, *fluctuans*, etc.), pondweeds (*Potamogeton epiphydrus*, *angustifolium*, *Richardsoni*, etc.),

than millions, of years, has not taken four times $1\frac{1}{2}$ millions of years (as Willis's estimate for a wind-dispersed tree would require) to become a series of associations in tolerable equilibrium.

The Canadian flora is also a direct refutation of Willis's assertion that "The hypothesis of youth (within the country) and area can only be accepted if one be prepared to accept with it the numerous absurdities to which it leads. It is very far-fetched, with no facts to

rest upon" (82, p. 198). The Canadian flora in a few thousand years has completely occupied an area of 1 to 4½ million square miles. This is not an absurdity nor even a hypothesis but a very plain fact; yet it involves plenty of "youth (within the country) and area" as well. If this simple case seems "far-fetched with no facts to rest upon" I can supply a dozen other cases, taken from the floras of Europe or other regions.

IMAGINARY DATA

It is quite clear, then, that many of the concepts with which Willis works are imaginary. Other botanists and zoologists, likewise, have found them so. Thus, Schonland finds that "Willis is fighting imaginary foes" (68, p. 454), and that in South Africa, as elsewhere, "In many cases the relation of 'Age and Area' can be *surmised*" (68, p. 462) without the intervention of a mathematical formula. And Holmes (46, p. 79) points out that Willis requires a world in process of being stocked with new species and not one in which old ones pass out as new ones come in, saying: "It is absurd to suppose that species . . . can expand and expand according to Age and Area without causing some unfortunate species of the region to retire"; and concluding: "When we attempt to make what Professor Tyndall calls the scientific use of the imagination in order to see where Dr. Willis's theory of species forming takes us, we find that we are led to a *reductio ad absurdum*."

Ridley regrets "that Dr. Willis seems to base so many of his arguments on statements made in books rather than on observations made in the field" (65, p. 567) and he gives numerous instances of erroneous deductions made from the data thus derived. He also emphasizes the fact that Willis's deductions regarding

the plants of Ceylon were based upon the representation of specimens in the Ceylon herbarium and had little to do with their actual rarity or abundance on the island. Both these objections are of far greater importance than the student who approaches the question from a purely theoretical standpoint is likely to realize. With only a few systematists working in a region the tendency, naturally, is to collect and preserve for study the interesting and rare rather than the commonplace species, and it is an oft-repeated truism that an herbarium or a museum is a collection of the exceptional rather than the ordinary forms. Any large collection illustrates this point. The Curly Grass (*Schizaea pusilla*) makes a dramatic appeal to a botanist of the northern hemisphere because it is the only species north of the Tropics of a prevailingly austral and ancient group; but the Cinnamon Fern (*Osmunda cinnamomea*) stirs no enthusiasm in the collector in eastern America. Consequently, we find in the Gray Herbarium 15 collections from Nova Scotia of the *Schizaea* from an area in the province 320 miles long, while the *Osmunda* is represented by only 6 collections from a much smaller area. By the method used by Willis the former would be called "common" or "very common," the latter "rare," but every child through the length of Nova Scotia knows the *Osmunda*, and it is safe to state that the only Nova Scotians who have ever seen *Schizaea* growing are those to whom Messrs. Nichols, Long or I have shown the plant. To be sure, Willis emphasizes that "my figures . . . refer to area occupied, not to commonness on the ground" (82, p. 192), to which statement Bateson pertinently replied that "the area 'occupied' by a species has immediately to be explained as meaning the area over which the

species *extends*" (4, p. 39); but even allowing, for the moment, that the "area over which the species extends" and not the "commonness" is of most importance, it must be obvious that the working out of "area" merely by the abundant representation of rarities in herbaria and the scant representation of the common species leads to the recognition of the "very rare" as *common*, the "very common" as *rare*. Surely the wholesale piling up of such errors must vitiate the result.

IMAGINARY SUPPORT

Willis seems to see in any one who mentions age, time, space or range in connection with plants or animals a supporter of Age and Area. Thus he attempts to show that two of the greatest men of the last century, Sir Charles Lyell and Sir Joseph Hooker, had really "discovered" Age and Area, simply because Lyell stated, and Hooker subscribed to the statement, that:

As a general rule, . . . species common to many distant provinces, or those now found to inhabit very distant parts of the globe, are to be regarded as the most ancient. Numerically speaking, they may not perhaps be largely represented, but their wide diffusion shows that they have had a long time to spread themselves, and have been able to survive many important revolutions in physical geography (54, p. 702).

Lyell's statement is common sense, but it is certainly far from Age and Area with all its implications; and when Hooker specifically said in the passage quoted by Willis, "we may not reverse the position, and assume local species to be among the most recently created" (47, p. xxv), he squarely opposed the teachings of Age and Area that local species are the youngest. Lyell and Hooker did not have an opportunity personally to disclaim sponsorship for Willis's views, but Tate Regan, the great authority on

fishes, did. At the meeting of the British Association at Hull in 1922 there was a general discussion of *The Present Position of Darwinism*. During the discussion Mr. Regan said:

Dr. Willis has shown on the screen a passage from my book on British Fresh Water Fishes, in which I state that dispersal takes time and proceeds at varying rates according to circumstances. From this he claims me as a supporter of the "age and area" hypothesis. . . . After careful consideration of the "age and area" hypothesis, I have reached the conclusion that it has no value (62, p. 164).

What could be more flat-footed than that?

UNVERIFIED IDENTITIES

Many accurate systematic botanists besides Ridley have pointed out that, in depending upon what he finds in books, instead of having a personal knowledge of the plants, Willis often falls into error, especially since he so often fails to check the identities with the best recent studies; and such an experienced student of the echinoderms as Clark, pointing out that the term *genus* is very inexact and that in comparing "genera" Willis often compares mixed elements, says: "I can juggle the genera of echinoderms . . . so as to lend apparent support to the Age and Area hypothesis, or I can redefine them so as to contradict it strongly, and in either case I can quote high authorities or give excellent reasons for my course" (17). One other instance of the need of accurate identification and correlation of groups before making sweeping deductions may be noted. In the passage quoted by Willis (91, p. 4) to indicate that Hooker was an early "discoverer" of Age and Area, Hooker said:

If this be true, it follows that consistently with the theory of the antiquity of the alpine flora of New Zealand, we should find amongst the plants common to New Zealand and the Antarctic Islands

some of the most cosmopolitan, and we do so in *Montia fontana*, *Callitriche verna*, *Cardamine hirsuta*, *Epilobium tetragonum* and many others.

Now everyone knows that Hooker drew his species with very broad limits and in 1853 he was more conservative as to specific lines than in his more experienced years; and, now, three-fourths of a century since the original statement, all critical systematists know that not one of the species mentioned by Hooker occurs in New Zealand nor (except perhaps the *Callitriche* in South America) in the southern hemisphere; yet I can find no indication by Willis that the determinations are open to question. *Montia fontana* (*M. minor* Gmel.) is characterized by having dull or opaque, plump back seeds conspicuously and closely covered with acutish to blunt tubercles and it is known only from Eurasia and western North America (see 34, p. 138, and t. 84); the plant of New Zealand, as any one can quickly see by examining New Zealand specimens, has much larger lenticular seeds which are highly lustrous and with flattened or obsolete tubercles. Its identity I do not know. *Cardamine hirsuta* is an annual of the northern hemisphere (chiefly Eurasia), the New Zealand plants which Hooker identified with it being three perennials with strikingly different habits, flowers, seeds, etc.; and so on with the *Callitriche* and the *Epilobium*. The New Zealand plants are *Montia* sp.; *Cardamine corymbosa* Hook. f. (Sir Joseph), endemic to New Zealand and Campbell I., *C. glacialis* (Forster) DC., of the antarctic and subantarctic regions, and *C. heterophylla* (Forster) O. E. Schulz (*C. debilis* Banks), of New Zealand and Chatham I. (see O. E. Schulz, Mon. Gatt. Card.); *Callitriche antarctica* Engelm. of the antarctic area and *C. Muellieri* Sond. of Australia, New Zealand and neighboring

islands; and *Epilobium Billardierianum* Ser. of Australia, Tasmania and the New Zealand region (see Haussknecht, Mon. Gatt. Epil.). In his *Flora of Stewart Island (New Zealand): A Study of Taxonomic Distribution* (86), Willis naïvely lists many other pseudo-cosmopolitan species. The New Zealand plant is assuredly not *Elatine americana* (see Fernald, Rhodora, xix, 12) but is presumably *E. gratioloides* A. Cunn.; the *Hydrocotyle* "americana" of New Zealand is the endemic *H. heteromeria* A. Rich.; the *Crantzia* "lineata" of New Zealand is utterly unlike the true *Crantzia* or *Lilaeopsis lineata*, which occurs strictly on the Atlantic coast of North America (see Fernald, Rhodora, xxvi, 93); the New Zealand representatives of the Eurasian *Luzula campestris* are the endemic *L. Banksiana* E. Meyer, *L. australasica* Steud. and others endemic to the Australasian region (see Buchenau in Engler, Pflanzenr. iv⁸⁶, 90-93); the plant of New Zealand which has long passed as *Potamogeton polygonifolius* is the endemic *P. suboblongus* Hagström (Crit. Researches on Pot. 182); *Festuca rubra* probably does not occur in New Zealand (see Hackel, Mon. Fest. Eur. where the extra-European range excludes the southern hemisphere); *Pteris aquilina* of New Zealand is certainly not the plant of Eurasia but, as everyone knows, is *P. esculenta* Forst. or, if you wish, *P. aquilina*, var. *esculenta* (Forst.) Hook.; and the New Zealand representative of *Polystichum aculeatum* is the wholly different *P. vestitum* (Forst.) Presl (See Christ, Ueber die australen *Polystichum*-Arten, Arkiv för Bot. iv, no. 12). Other cases, like those of *Spergularia media*, *Juncus effusus* and *Deschampsia cespitosa*, groups with sharply defined geographic segregates. I have not attempted to check, but any critical systematist will realize, without argument,

that the New Zealand plants will prove quite distinct from the European. With 100 per cent of error in Willis's identifications of such plants of New Zealand as I happen to know something about, what hope can there be that all the other reputedly wide-ranging species would pass unchallenged a critical systematic inspection? In other words, to resume the original thread, not one of the four European species mentioned by Hooker (and after him by Willis) occur in New Zealand, but they are there represented by species endemic to New Zealand or to the subantarctic region. If as "cosmopolitan" species they demonstrated by their broad ranges in New Zealand the truth of Age and Area, do they now as endemic or near-endemics suddenly restrict their ranges in New Zealand? In almost the same paragraph Willis says: "I must consider myself very fortunate in having finally discovered that the effects of age were sufficiently clear to be arithmetically expressed" (91, p. 6). As an illustration of mathematics applied to problems of plant distribution, the occurrence of "cosmopolitan" species in New Zealand, involving an error of 100 per cent, is unfortunate.

INACCURATE GEOLOGICAL DATA

Other features of Willis's work which at once demonstrate that no reliance can be placed upon the precision of his method and consequently upon the soundness of his deductions are numerous. One case in particular is very pathetic or very ludicrous according to the degree of compassion one may feel. Professor James Small contributes a chapter on *Age and Area, and Size and Space, in Compositae*, in which he develops his ideas of the evolution of the group. Because of the great expansion of the genus *Senecio* in the northern Andean region he localizes

the evolution of the Composites through that genus in the Andes in upper Cretaceous time. But, as Berry remarks, the fact that Small "by age-and-area methods, finds that the great alliance of the Compositae originated in the mountains of northwestern South America at a time when there were neither mountains nor even land in that region, but seas, does not add to my confidence in the general method" (7, p. 547); and Bateson politely said: "The inclusion of the chapter on the Composites reflects more credit on Dr. Willis's candor than on his scientific judgment" (4, p. 41). The fact is, that the great elevation of the Andes, where *Senecio* now has its phenomenal development, did not occur until the Pliocene and early Pleistocene (69, p. 923; 6, p. 8); and, although Willis finds Small's work a "remarkable verification" (91, p. 116) of Age and Area, opponents might be tempted to point out that, since it is based on a colossal error, it is *naturally* a verification of Age and Error!

WILLIS'S COLLABORATORS

A chapter is contributed by de Vries, who finds Willis's work "the one great proof, which the mutation theory still wanted for its acceptance in the field of systematic zoology and botany" (91, p. 227). Nevertheless, I have seen no indication of the systematic zoologists and botanists swinging in a body to the mutation theory! Guppy has a short chapter in which he discusses the *Position of the Age and Area Theory*; and Mrs. Clement Reid, although admitting that "the evidence of universal extinction of species furnished by the pages of palaeobotany is incontrovertible" (91, p. 143) and that "more species found in the older deposits are extinct, than in the newer" (91, p. 144), stands almost if not quite unique among paleontologists

in conferring her benediction on Willis's views.

PREDICTIONS BY AGE AND AREA

As to the reiterated insistence by Willis that all his provisos must be kept in mind, but that in spite of their negating tendency Age and Area is a hypothesis by which one may discover new facts, and that *all* predictions made by it have proved to be correct, Bateson justly remarked: "Repetition of the bald assurance that Age and Area is the true faith should be unnecessary. A judicious advocate would leave that conclusion to flow more quietly from the evidence . . . the reader's scepticism is thus instantly aroused" (4, p. 39). As to predictions made by others, Willis seems to take comfort in the two made in America: "Taylor has studied the endemics of New York and of the Bahama islands, obtaining results that harmonize quite well with the general theory of Age and Area" (91, p. 64). Willis admits, however, that in case of the Bahamas "it was noticed that the difference usually seen between the distribution of the endemics and the wides was not nearly so large as usual." And as to the endemics of the region of New York, the facts are illuminating. Taylor (75) recognized 22 species as endemic to his area. But of these, 1 extends south to Florida, 1 to South Carolina, 1 to North Carolina, 2 to Virginia, 1 to Maryland, 1 beyond Taylor's limits in Pennsylvania and 1 eastward to Rhode Island; 2 are apparently local hybrids and 1 (*Salix squamata*) was simply an aberrant individual of the wide-spread *S. discolor*. These rejected "endemics" of the New York region are as follows: *Calamovilfa brevipes* (North Carolina acc. to Hitchcock, Gen. Grasses U. S. 125); *Juncus caesariensis* (Virginia, Grimes, Rhodora, xxiv, 149); *Uvularia nitida* (South Carolina, as

the scarcely separable *Oakesia puberula* acc. to Robinson and Fernald, Gray Man. ed. 7, 286); *Salix squamata* (see Schneider, Journ. Arn. Arb. ii, 3); *Dentaria incisifolia* and *D. anomala*, strongly suggesting hybrids, the latter thought by its author to "have had a hybrid origin" (Eames, Rhodora, v, 217); *Prunus allegheniensis* (see Taylor, Torrey, xvi, 18); *Hibiscus oculiroseus* (Rhode Island, Sanford, Rhodora, xxvi, 88); *Ludwigiantha brevipes* (Virginia, Rugel, 1840, in Gray Herb.); *Dendrium buxifolium* (Florida acc. to Small, Fl. Sc. U. S. ed. 2, 822) and *Senecio Crawfordii* (Maryland, Standley, Rhodora, xxi, 117). That leaves, as endemic to the region within 100 miles of New York City, 2 freakish plants (*Hypericum Bissellii* and *Pyrola oxypetalum*) which were exterminated by their discoverers, 3 true endemics of the comparatively ancient Pine Barrens of New Jersey, and 6 localized species occurring at the border of the now submerged Cretaceous and Tertiary continental shelf, the latter region before completely going under the sea having left a relic-flora along the margin of the continent eastward to Nova Scotia and even to Newfoundland (see 28, pp. 149-162; 31, p. 168; 50, chap. viii). These 6 endemics are quite possibly as ancient as those of the Pine Barrens. At any rate, like the endemics of the Bahamas, they are not in any way proof of Age and Area.

I personally spent several weeks in a test of Age and Area, taking for my test two regions upon which I had worked during a quarter-century, Newfoundland and the Gaspé Peninsula. The resulting figures upon superficial examination "seem very reassuring to supporters of Age and Area. . . . But . . . the actual facts are squarely opposed to Age and Area; for in both Gaspé and Newfoundland the most ancient flora of each region has the most limited range and also the

most limited 'wide' range, while the youngest flora to arrive in each area has two or three times the range both inside and outside these regions" (32, p. 563). Calvert, likewise, has attempted to get satisfaction out of Willis's method by applying it to the distribution of insects in various regions but finally concluded: "I fail to find the key to the origin and evolution of species with the ease which Dr. Willis's commendation of Age and Area would lead me to expect and which I would welcome if the key but turned in the lock" (13, p. 229).

So much for the general question; now for some of the correlaries and details.

SIZE AND SPACE

Seeking to catch the popular fancy, Willis hit on what he calls his "alliterative series." The trick is an old one but it should not take the place of plain facts and sound reasoning. The ear is quickly caught by such pairs as Age and Area, Antiquity and Amplitude, Rank and Range, Size and Space and Size and Surface, and Willis specially selects "Age and Area" and "Size and Space" (*alias* "Antiquity and Amplitude") for immortalization. It is worth noting, however, that he is somewhat confused in tracing the relationship of "Size and Space." Sometimes he speaks of it as the child or "extension" (91, p. 113) of "Age and Area," at others he states that "Age and Area" and "Size and Space" are *twins* (91, p. 107). Since Willis, himself, was the only witness of the birth of both of them, it is regrettable that in a question dealing with relative ages such contradictory evidence should have crept in. Willis's statement of Size and Space is:

Keeping to the same circle of affinity, the larger families and genera will be the older, and will therefore occupy the most space. This, however, involves a break with the long current idea, that the

larger families and genera are the successful ones, the smaller the (comparative) failures (91, p. 113).

Or in more concise form he says: "The larger a genus, the older will it be, *within its own circle of affinity.*" And, extending his ideas, he applies the same formula to groups of related species and to related families and always finds his own predictions successful. "Species and genera are endemic simply because they have not yet had time to spread abroad" (91, p. 183). "The supposition that endemic genera are usually relics . . . must be ruled out of consideration" (91, p. 110). Species, according to Willis, originate in regular mathematical progression, each genus or series throwing off a species at a regular interval, and the spread of the species is radial from the center of origin; and he believes that the facts of distribution can be expressed by a "hollow curve."

The hollow curve is apparently a universal principle of distribution, whether it be distribution in space—geographical distribution—or distribution in time—evolution. A species as it increases in age expands its area, while a genus increases its number of species, the younger occupying smaller and smaller areas, usually within the area of the first species, until that becomes very large (91, p. 199).

REFUTATION BY PALEONTOLOGY

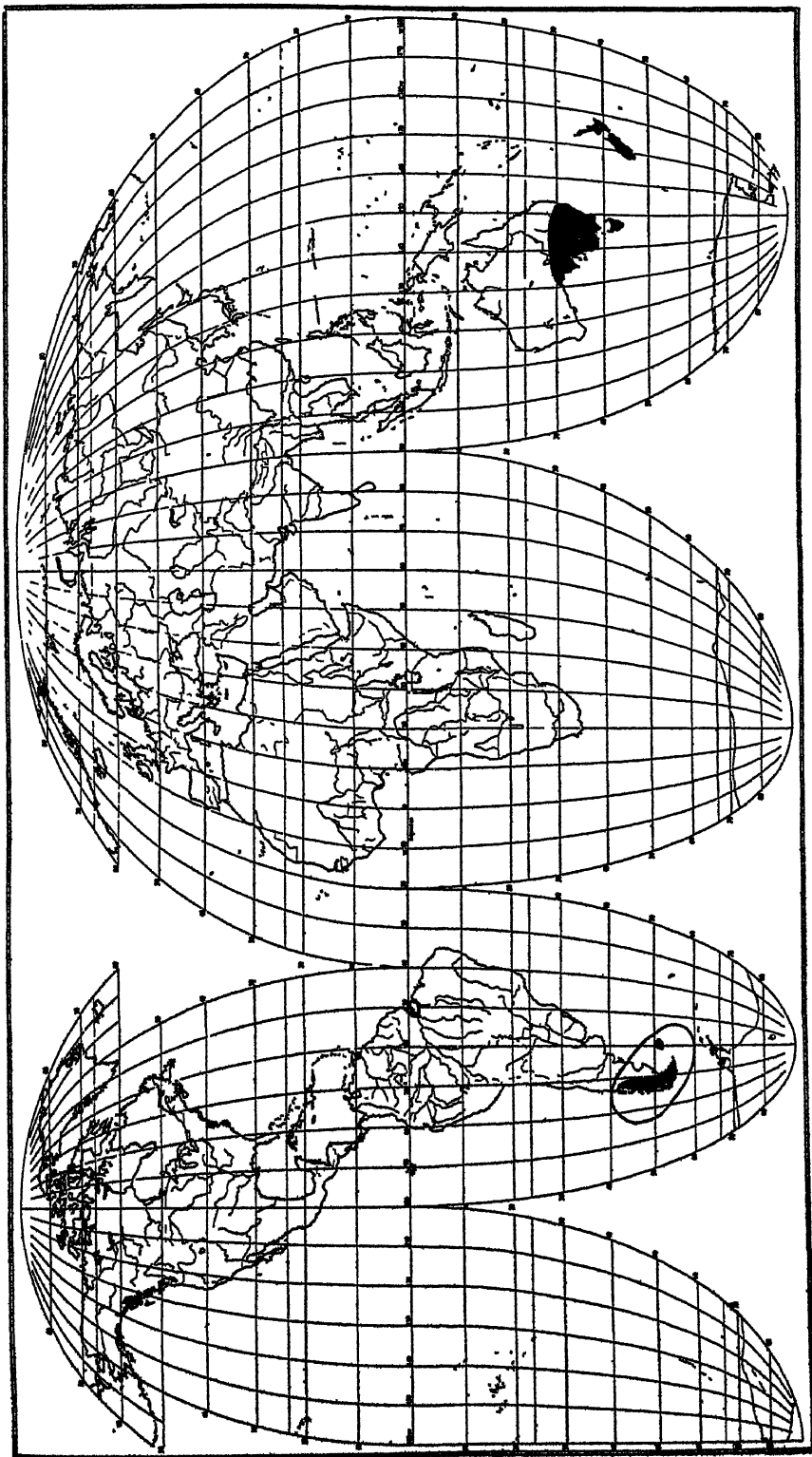
It is thus again obvious that Willis and his mathematical friends live in a theoretical world and that, although going through the form of admitting geological, ecological and climatic changes, they do not really comprehend how vast and all-controlling the actual historic and edaphic factors have been. Immediately they were confronted by the paleontologist, and such an unchallenged authority as Seward pointed out, that in the "confers and ferns, study showed that the forms existing now in restricted areas were the oldest and not the youngest"

(70); and Berry said: "The statement that the dying out of species is a rare event is overwhelmingly opposed by all the facts of paleontology and by all the facts of history unless its adherents are prepared to accept the Mosaic cosmogony . . . the probability is very great that the present flora of the globe represents a minute fraction of the extinct floras . . . in all the orders of plants that are prevailingly aborescent the geologic distribution where it is known is found to have been more extensive than the present distribution. . . . So-called monotypic genera, whether plant or animal, at least in the majority of cases, are relicts of a once wider distribution" (5, p. 540). Somewhat later Berry amplified his statement by publishing convincing maps of past and present ranges of many genera (6, 7). Ridley, along the same lines, also pointed out, that the most extensively distributed flowering plant in the world today is the Reed, *Phragmites communis*, with a good dispersal mechanism (plumed fruits) but unknown as a fossil earlier than the Pliocene; while the vast ancient group of Cycads is now reduced to about 80 species, each confined to a very limited area. Similarly the Nipa Palm, which in the Eocene grew in Europe, Africa and North America, is today confined to shores of "the Indian Ocean from Ceylon and Bengal, down the Malay Peninsula to North Australia and the Caroline and Solomon Islands, not having got so far as the Mascarene Islands, peninsular India, or Polynesia, in spite of its abundance as a drift plant . . . always to be seen drifting in Malayan seas. It . . . requires tidal mud . . . but there must be tidal-mud rivers in Samoa, Africa and America" (66, p. 29).

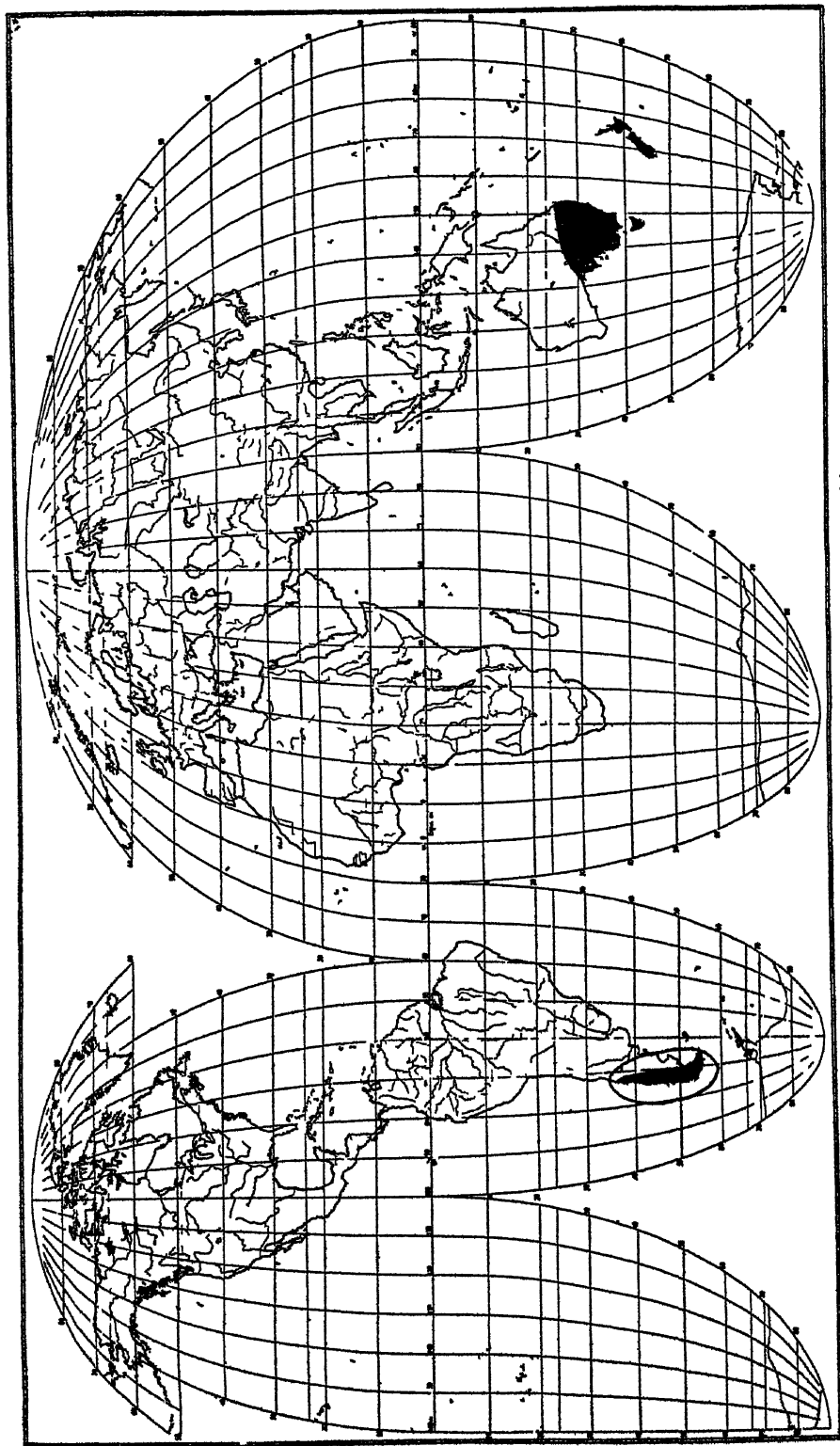
But to these and all other parallel cases brought forward from paleontology Wil-

lis merely replied: "in dealing with them from an Age and Area point of view, one must include the 'fossil' area" (91, p. 94).

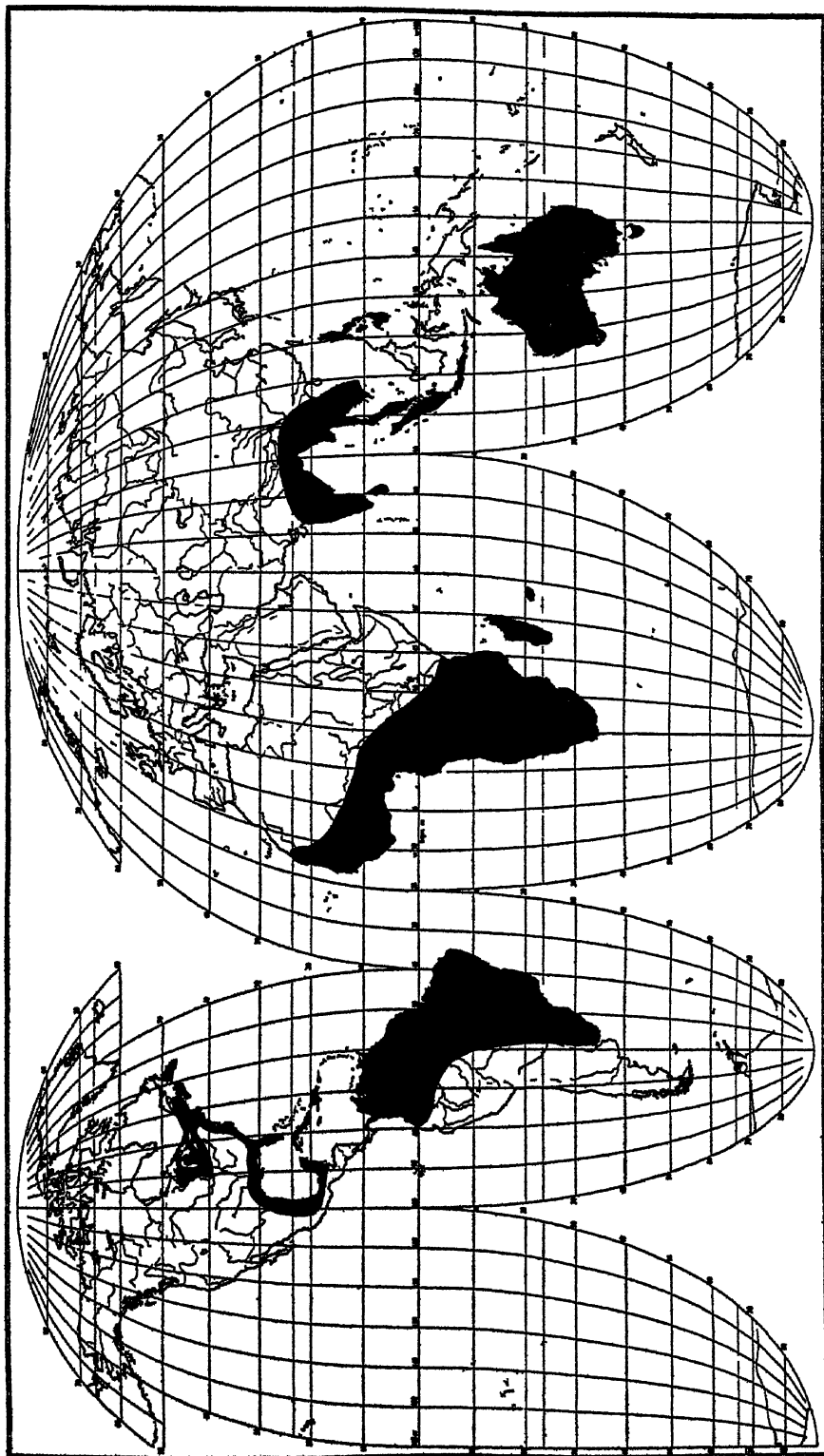
That, of course, is a quibble, as has repeatedly been pointed out. How can we know the "fossil" area of the vast majority of plants, which, occurring today as obvious relicts of former wide dispersal, must have had a fossil area? The woody "Veronics" of New Zealand differ in every important detail from the essentially boreal herbaceous Veronics and constitute the genus or subgenus *Hebe*, which has characters more primitive than in true *Veronica* (see 59, p. 2; 32, p. 571). *Hebe* has most of its present species in New Zealand, with a few species in Australia and Tasmania, and four of the New Zealand species also on the Falkland Islands or in southern Chile. The present range of *Hebe* (map 2) is almost identical with the range of such genera as *Nothofagus* (map 3), whose ancestry is traced back to the Cretaceous (6, chap. xii), and very nearly that of *Araucaria* which extends much farther back; yet no fossils of *Hebe* are identified. The ranges of the *Eriocaulaceae*, *Xyridaceae* (map 4) and the *Halorrhageae* coincide in their larger features with the present distribution of the Persimmon, *Diospyros* (map 5). "In that grand display of dicotyledonous genera which, during the mid-Cretaceous replaced the old Mesozoic flora . . . we find unmistakable evidence of the abundance and wide distribution of species of *Diospyros*" (6, p. 257), which covered the northern hemisphere quite to the Arctic. He would be a bold man who would say that, simply because they are herbs and consequently have left no fossils, *Eriocaulon*, *Xyris* and *Halorrhagis* are not quite as old as *Diospyros*; or, similarly that the herbaceous genera *Symplocarpus*, *Podophyllum* and *Mitchella*, sharing south-eastern continental North America and



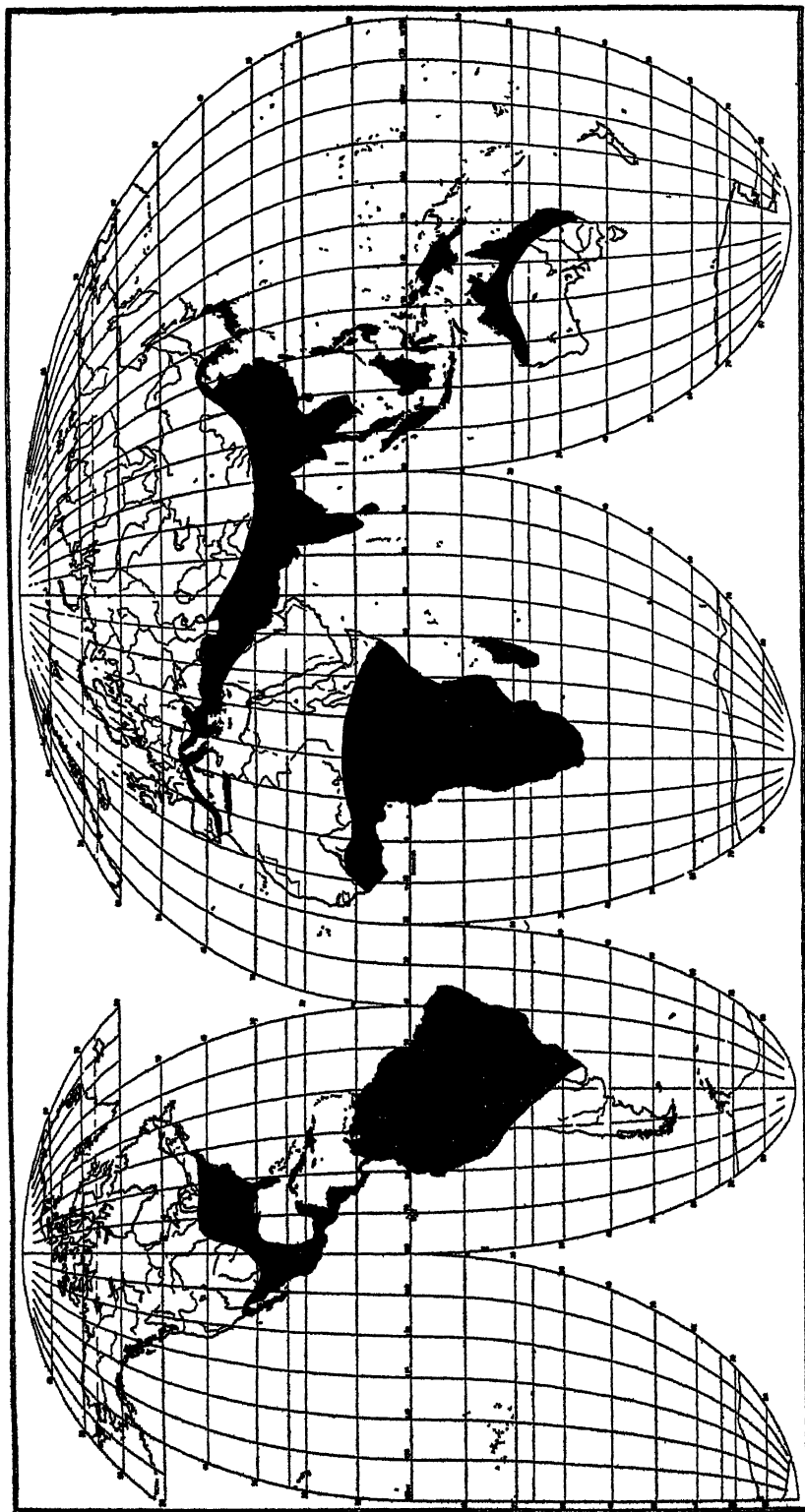
MAP 2. RANGE OF HERE



MAP 1. PRESENT RANGE OF NOTHOFAGUS, AFTER BERRY (6)



MAP 4. RANGE OF XYRIDACEAE



MAP 5. PRESENT RANGE OF DIOSPYROS, AFTER BERRY (6 AND 7)

southeastern continental Asia, are not as old as their ligneous associates in the same areas, *Liriodendron*, *Sassafras* and *Liquidambar*. These and many other ligneous genera of the same ranges are well known as Mesozoic or early Cenozoic types. But what is the fossil range of their herbaceous associates? We can safely infer it but, after all, we can only infer it.

AGES OF LARGE AND SMALL GENERA

Willis's idea, that the larger genera are the older, the smaller closely related genera the younger, gathers force only by his perpetual repetition of it. But those who have an intimate knowledge of the morphological and phylogenetic, as well as the geological evidence make exactly the opposite decision. The paleontological evidence is decisive; the evidence from living groups is quite as good. The very numerous genera which formed the Mesozoic and early Cenozoic flora, then extending around the northern hemisphere but now reduced to small remnants in eastern Asia or eastern North America or to limited areas on both continents, have been repeatedly marshalled as evidence. After studying the ranges of the largest genera of dicotyledons of temperate North America in relation to Age and Area I summarized my conclusions as follows:

Now, by Willis's interpretation these large genera are large because they are old, the small genera small because they are young. Naturally there is no *absolute* proof of this or of any other hypothetical proposition. But does not the whole matter leave the realm of hypothesis and enter the realm of demonstrable fact when we consider the geological history of the regions involved? It is generally conceded, I believe, that the most ancient living floras are now concentrated largely in Australia, New Zealand and South Africa. It is also generally admitted that the Mediterranean basin, including a broad belt of North Africa and the

country across Egypt and Syria, and, again, the great Austro-Russian basin extending southeastward to Persia were Tertiary sea bottom; similarly, by far the greatest part of the prairies, plains, and arid basins west of the Mississippi owe their present condition to Tertiary and even more recent geological activities. In other words, these regions were largely unavailable to their present floras millions of years after most of the groups which now distinguish Australia and New Zealand were at the height of their development. If, then, the largest genera of our flora, which are also overwhelmingly the largest genera of their own "circles of affinity," are, as Willis maintains, large because they are the ancient genera, is it not singular that *Eriogonum*, *Crataegus*, *Rubus* § *Eubatus*, *Lupinus*, *Astragalus*, *Oenothera*, *Galiea*, *Phacelia*, *Pentstemon*, *Solidago*, *Aplopappus*, and *Artemisia* should have not even a single species associated with the ancient types which inhabit Australia and New Zealand, and that only 0.02 of the total species of *Potentilla*, *Euphorbia*, *Aster* and *Erigeron* should have reached those lands? Is it not equally noteworthy that, with the exception of *Crataegus* and the blackberries (*Rubus* § *Eubatus*), all the *largest* genera of the temperate North American flora should be centralized upon the Tertiary sea bottoms (relatively youthful country) of the Mediterranean and Austro-Russian basins of the Old World and in the vast area of youthful country west and southwest of the Mississippi? The blackberries are most virulent in central and western Europe, a region available to plants only since the Pleistocene glaciation, but likewise in the glaciated region and the Tertiary coastal plain of eastern North America. *Crataegus* has its phenomenal development in the eastern United States and southern Canada, where it must have produced a multitude of its species in post-glacial time.

It should be perfectly obvious that these genera and likewise such overwhelmingly large genera of Europe and southwestern Asia (but not of Australia and New Zealand) as *Dianthus* (200-300 Eurasian species), *Silene* (300-400), *Verbascum* (150-200), *Cousinia* (150), *Centaurea* (200-300), and *Hieracium* (600-700) are really very young, or, if geologically old (*Crataegus* and *Rubus* for example), they have been encouraged by modern conditions to rapid multiplication. And if we estimate success of plants by their ability to cover country, to take care of themselves, and to multiply their variations to the bewilderment of the best systematists, then these are surely successful genera. No society for the protection of native plants has thought it necessary to urge protection for *Eriogonum*, *Crataegus*, *Rubus* § *Eubatus*, *Euphorbia*, *Solidago*, *Artemisia*, *Centaurea*, and *Hieracium*; but there are plenty of people (including many

botanists) who would be glad to have them suppressed.

The genera of eastern America which need scrupulous protection are the woodland herbs of the Alleghenian forest, the genera which we largely share with Japan and China and which are consequently among the oldest plants now living on the North American continent. These are chiefly ditypes, with one species in eastern America, one in eastern Asia, though some of the genera have more than two species; but, while the systematist shrugs his shoulders and waves you away if you bring him for determination a collection of the youthful species of *Lupinus*, *Oenothera*, *Aster*, or *Artemisia*, he can give a prompt and explicit determination of *Caulophyllum*, *Podophyllum*, *Dicentra*, *Panax*, *Cryptotaenia*, *Epigaea*, *Chimaphila*, and *Mitchella*—and why should he not? These are genera of the eastern Asiatic-eastern American forests; and they are absolutely segregated genera with no complications of freely intergradient species, not, as Age and Area asserts, because they are young beginners, but because they are old veterans (32, pp. 568-570).

If these cases are not conclusive, let us consider the tribe *Cariceae* of the Sedges. Kükenthal (53) recognizes four genera. *Carex* is world-wide, with 798 species, which in view of more recent studies can safely be extended to 850. *Uncinia*, with 24 species, is on the subantarctic islands (the Falklands, Sandwich Islands, Amsterdam I., Tristan da Cunha, Kerguelen, St. Paul, Macquarie, Auckland and Campbell) thence extending north into South America, New Zealand, Australia and New Guinea. North of New Guinea in the East and of South America in the West the genus is unknown except for 1 species found the length of South America and slightly northward into Costa Rica, another extending from South America to Mexico and Jamaica; but the problematic *Carex microglochin* Wahlenb. (described from mountains of arctic Lapland) is so poorly distinguished from *Uncinia* that one of the greatest students of the *Cyperaceae*, the late C. B. Clarke, wrote: "I feel sure that, had *C. microglochin* been found in the southern hemisphere in-

stead of in the northern, authors would have placed it without hesitation in *Uncinia*" (18, p. 374). Now it so happens that *C. microglochin*, or a plant scarcely separable from it, actually has been found in the southern hemisphere, in Patagonia and Fuegia (18, p. 402; 53, p. 109); and in the northern hemisphere it has the thoroughly typical disrupted range of a relic-species, chiefly in areas whose floras were not destroyed by the latest advances of the continental ice-sheets of the Pleistocene. The third genus is *Kobresia*, with 29 species, 27 of them confined to the ancient flora of Asia, the other 2 also found in Asia but also with a highly disrupted relic-distribution around the northern hemisphere; and the fourth genus is *Schoenoxypgium*, with 6 species all endemic to South Africa.

Now by Age and Area, the vast genus *Carex* (850± species) is the oldest of the four because today it is world-wide and overwhelmingly the largest group; *Uncinia*, *Kobresia* and *Schoenoxypgium* should be very much younger because they are more localized and with far fewer species. Nevertheless, no critical student of the group hesitates for an instant in believing that the presence of the rachilla (the axis of a spikelet such as is found in most sedges) in all three of the small and localized genera and the mostly open spathe in *Kobresia* and *Schoenoxypgium* are primitive characters; and that the great bulk of true *Carices*, in lacking the rachilla (having the female spikelet reduced to a single flower) and in having the margins of the spathe united to form a closed pouch (the perigynium or utriculus), are later in origin than the other three genera.

To be sure, there are a few *Carices* which, in having the rachilla, show transitions to the more primitive genera;

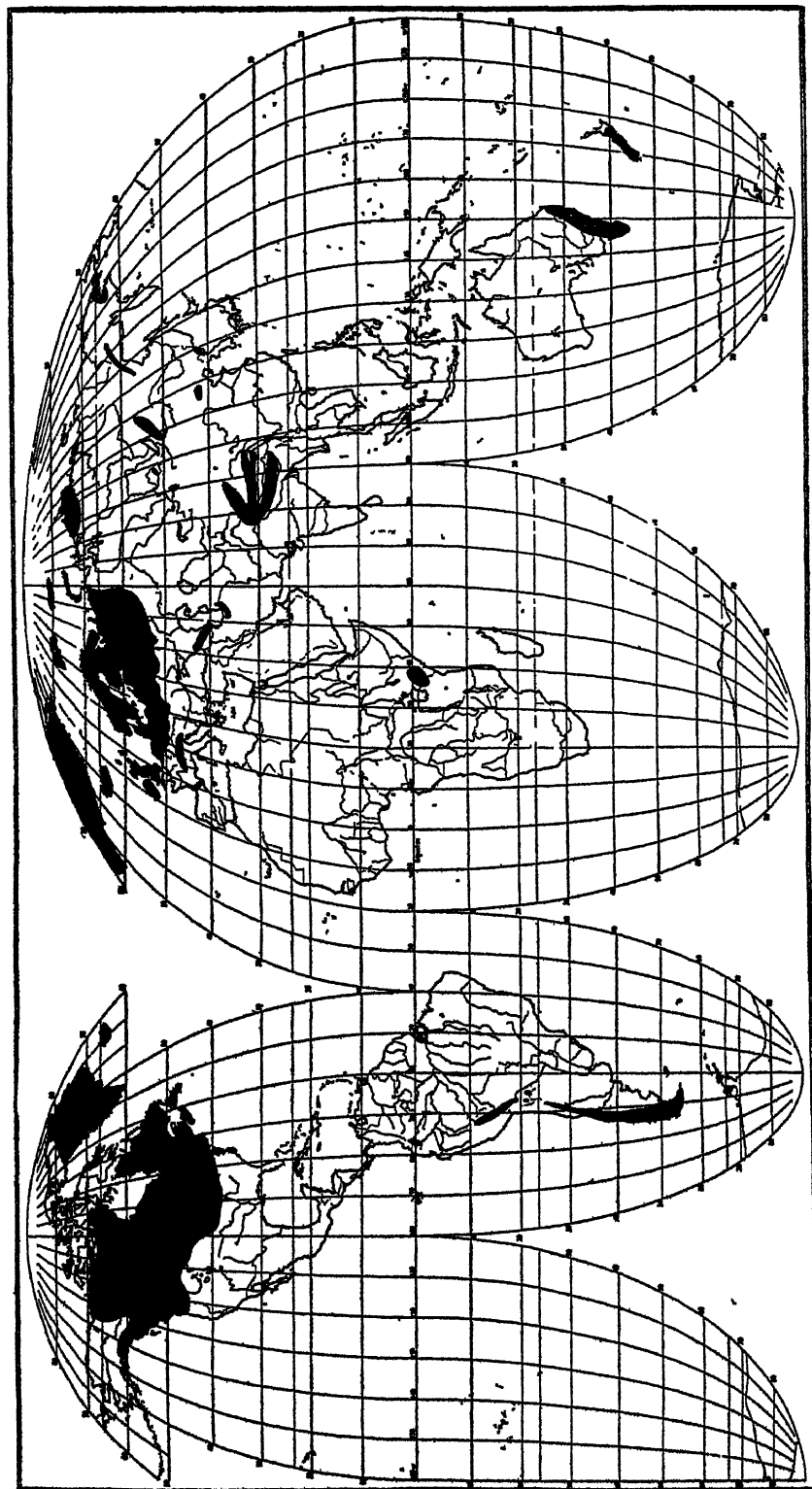
but, when the present geographic ranges of these most primitive of *Cariceae* are checked, they at once become illuminating. The case of *C. microglochis*, which is practically as good an *Uncinia*, has been discussed. Taking Boott's *Illustrations of Carex* (11) as the handiest guide, we find there illustrated (in a total of 600 plates) 17 other species which regularly have the rachilla present and which are therefore considered primitive. 3 of these are now treated as *Kobresias*; thus leaving 14. Other such species are now known but their geographic isolations are wholly consistent with those here discussed. Of these 14, 3 are rare alpine endemics of western and central Asia, 1 of high mountains of Eastern Africa, 1 of the Macronesian islands, 1 of alpine regions of Pacific North America; 1 (*C. filifolia*) characteristic of western North America but isolated on the high unglaciated Torngat Mts. of northern Labrador (see 33, p. 316); 3 confined to southern South America; 2 to Australia, Tasmania and New Zealand; 1 (*C. pyrenaica*) to remote alpine regions of the northern hemisphere and to New Zealand, and the last is *C. Fraseri*.

Carex Fraseri, a very rare and local plant of mountain woods of Virginia, West Virginia, North Carolina and eastern Tennessee, is, as demonstrated by Holm, so primitive in its morphological and anatomical characters as to be "almost unique in the family of the *Cyperaceae*" (45, p. 127). In fact, so unique and primitive is the plant that there is every reason to follow Mackenzie in distinguishing it as a monotypic genus, *Cymophyllus* (55, p. 441). *Cymophyllus*, like the Green Dragon (*Arisaema Dracontium*), the Skunk Cabbage (*Symplocarpus foetidus*), Ram's-head Ladies Slipper (*Cypripedium arietinum*), the hickories (*Carya* or *Hicoria*), the tear-thumbs (*Polygonum* or *Tracaulon*

arifolium and *sagittatum*), Indian Lotus (*Nelumbo*), the Tulip Tree (*Liriodendron*), the May Apple (*Podophyllum*) and hundreds of others, is unquestionably a relic of the late Mesozoic or early Cenozoic flora so tellingly pictured by that master of vivid reconstruction, Guppy. In congratulating the American student of plants upon the abundance of these ancient types still living, Guppy projects a dream:

In the woods around him were growing the Liquidambar, the Sassafras, and other shrubs and trees that had flourished in the Mesozoic ages in the spot where he was standing. Their remains crowded the Cretaceous deposits exhibited in the cliffs near by. Specimens of the past and of the present were in his hands. Though the difference in kind was very slight . . . the difference in time, measured in human lives, amounted to eternity. It is a story of perpetuity rather than of change. . . . He begins with the cosmopolitanism of such types in the Cretaceous age and he ends with their more restricted distribution and somewhat greater specialization now. . . . Those old genera become the genera of today; and the genera of today, though the genera of a thousand ages, are "but as yesterday" in the history of flowering plants (42).

This prolonged discussion of the situation in the *Cariceae* is here given because it is so typical of many large groups, the small and primitive or unique genera or sections chiefly localized in regions which have largely escaped the depleting agencies of Pleistocene continental glaciations or other comparatively recent wholesale calamities, the overwhelmingly large and more modern series abounding both with the ancient floras and in those which must have arisen in Pliocene, Pleistocene or in some cases even post-Pleistocene time. That Willis might think the ancient small genera of Asia young would be natural, since he closes his eyes to the consensus of geological evidence that, in the Pleistocene, Asiatic glaciation was associated primarily with high altitudes. The latter fact comes out sharply in a



MAP 6. MAXIMUM EXTENSION OF PLEISTOCENE GLACIATION, AFTER SCHUCHERT (69), GRABAU (40) AND FERNALD (33)

map of the maximum Pleistocene glaciation of the northern hemisphere (map 6) Willis, ignoring such evidence, speaks without a word of qualification of "China, where the influence of the last glacial period was severely felt" (91, p. 88). Naturally, if one ignores all geological and morphological facts, he can at will prove anything either young or old; but that Guppy, who wrote the pregnant passage above quoted, should give his approval to Age and Area is certainly amazing.

Another case, which Willis cites, is instructive. Taking the 28 largest genera in the world, Willis states that 16 are cosmopolitan, 5 cosmo-tropic, 4 tropical American, "and *Quercus* Old World [surely *Quercus* grows in the New World, Trelease (77) recognizing 372 American species], leaving only *Erica* and *Mesembryanthemum*, whose large number of species is correlated in both cases with the fact that they grow in South Africa, where the extreme conditions [Is this mathematical saltation?] seem to tend to produce large numbers of species" (91, p. 117). Now, in regard to *Erica*, Schonland shows, by a detailed tabulation of the 5 subgenera, 41 sections and approximately 1000 species of the genus in South Africa, that "the whole theory [of Age and Area] as applied to this case tumbles to pieces— (1) When we analyze groups of species; (2) when we take into account allied genera which appear to be derived from the genus *Erica*; (3) when we take into account the distribution of the *Ericaceae* generally, and of *Erica* in particular, which seem to prove that *Erica* has arisen in the Northern Hemisphere. There is not a single fact known which indicates southern origin. It must have come to us through the mountains of tropical Africa." And, after discussion of the details, Schonland says:

a theory. They show, however, plainly in the first place that when we come to bed-rock of Willis's "Age and Area theory" by comparing a number of closely allied species of the same ecological type, the present distribution of the South African species of *Erica* does not fit in with a mechanical rule such as Willis thinks he has discovered as governing the distribution of plants. The species which occur at widely separated stations or closely allied species in similar position, both of which will be found in these brief remarks, are particularly interesting, as previously pointed out, because if they disappeared from either of their distant stations their whole position in a scheme of distribution would be completely altered. . . .

When we come to the tropical African species we again find little to help us in gauging age by area. . . .

Before further commenting on these facts we must glance at the distribution of African genera allied to *Erica*. . . . The huge gaps in the distribution of these derived genera are particularly noteworthy. If we knew the genus *Erica* and its allies only, we might come to the conclusion that it has dwelt longest in South Africa and that all species outside South Africa are outliers. Thus we would assume that the development has taken place in a northward direction. This assumption probably would to a certain extent be correct, but on considering the other *Ericaceae* we see that the original current of distribution has been in just the opposite direction. However, no "Age and Area theory" can disentangle these two opposite currents except in the vaguest sort of way. Willis, "with the aid of a prediction of the bearings of Age and Area upon the subject," came to the conclusion, as regards the New Zealand flora, that the number of endemic species in any genus would rise "gradually to a maximum at or near the point where the genus entered New Zealand in the first place." Applying this prediction to the genus *Erica* in South Africa, this point would be a part of South-west Cape Colony west of George, where not only a large number of endemics are massed, but where, moreover, the greatest diversity owing to formation of subgenera and derived genera is to be found; but I fear no contradiction when I assert that it is certainly not the place where the genus *Erica* entered South Africa, or where it originated, and thus again Willis's theory breaks down (68, pp. 465-471).

AGES OF ENDEMICIS

In regard to Willis's idea that the endemic genera and species are young begin-

those which occur in the neighborhood of their allies, for which Ridley would retain the term *Endemics* "which signifies those who live with their people"; and those which are far removed geographically from their allies, the survivors of a lost flora, for which he proposes "the name *Epibiotics*, which signifies survivors" (67). The former or true endemics are naturally younger than their ancestors. No one questions that. Whether they are more numerous or less numerous than the epibiotics I cannot say. Willis says they are more abundant and certainly the vast numbers of somewhat localized species of *Astragalus*, *Artemisia*, *Crataegus*, *Rubus*, etc., give support to his contention; but these are surely very young species. In fact, some botanists question whether they are species at all or whether they will reach sharp specific segregation within the era of human history. Such groups as these will be further discussed in another connection.

In many floras a large proportion of the genera, although not themselves endemic genera, are represented only by endemic species. Willis maintains that these are young species, which have been given off by some wide-ranging species which was the first of the group to arrive on the ground. This situation has been specially noted for New Zealand, where 43 per cent of the genera are said to be non-endemic or wide-ranging genera which in New Zealand are represented only by endemic species. Since Willis's theory states that the species which have a wide range outside a given country will also have a wide range in every country they inhabit (because they are assumed to be the oldest), Sinnott (73, p. 575) raises and pushes the query: What has become of the wide-ranging species of nearly half the genera of the New Zealand flora which were the first to arrive there?

If they ever did arrive, they are now completely "swamped out" and Willis's theory, that they must now be the widest-ranging species in New Zealand, falls completely to the ground.

Willis himself, without seeming to understand them, supplies figures which, checked with the most familiar facts of geological history, completely refute his claims. To be sure, I am aware that his figures cannot always be accepted at their face value, for as I have elsewhere been obliged to point out, "in arguing that there are more endemics in tropical than in temperate regions he makes what would seem a clinching assertion: 'North-temperate America has perhaps 400, but Ceylon alone has 800 endemics, and Brazil perhaps 12,000' (91, p. 89). In view of the 1000 endemic grasses recognized in temperate North America, the 400 Carices, the more than 300 Cruciferae or Umbelliferae, the full 100 Malvaceae, to say nothing of *Eriogonum*, *Crataegus*, *Astragalus*, *Euphorbia*, and all the rest, the utter folly of attempting to prove anything by such wholly unreliable statistics must be apparent" (32, p. 571). But, even taking his figures as presumably near the facts, we find, for instance, that Great Britain has no endemic genera, Japan 69 (91, p. 170) and that of the latter 54 are monotypes (of a single species) and most of the others ditypes, with only 1 genus having as many as 8 species (91, p. 175). We further find that, "Whilst the largest number and proportions of endemics are chiefly in the more southern countries, there are also large numbers and proportions in several of the northern, e.g. in Mongolia, California, the region about the Mediterranean Sea, etc. There are a few endemics on the west coast of Europe, the Alps contain about 200, and Italy about the same; and the Iberian peninsula contains about 800, or

roughly the same as Ceylon" (91, p. 149).

In view of the fact that Great Britain was severely denuded by the Pleistocene glaciers and that, for the most part, her flora has occupied the islands only a few thousand years, it should surprise no one to find the British endemic genera totaling 0; but Japan, undisturbed during the Pleistocene, has 69 endemic genera, mostly monotypes. Yet Willis calls the monotypic genera young, because they have only 1 species. It needs no argument, in view of the proved antiquity of many Japanese monotypes, to show that he here has no ground to stand on. Similarly with Mongolia and China, famous for their great number of monotypic genera. Willis, as already noted, refers to "China, where the influence of the last glacial period was severely felt," but the statements in regard to the Pleistocene in southeastern Asia, by such geologists as James Geikie (37, p. 697), Schuchert (69, see map 6) and Grabau (40), are sufficient to show that those who ascribe the great number of Chinese and Mongolian monotypes to *lack of universal glaciation* and consequently long existence in the region have the geological evidence on their side. Again, can it be that the antiquity of the Iberian tableland, essentially undisturbed since the dawn of angiosperms, has nothing to do with the occurrence there of 800 endemics? From Cretaceous time (map 7), when an arm of the Mediterranean almost severed Iberia from France, through the Eocene (map 8), when continental Europe was almost obliterated by the sea, through the Oligocene (map 9), when the sea wholly separated Iberia from other lands, on through the Pliocene (map 10), when the surrounding seas of Europe were still extensive, and through the Pleistocene (map 6), when the ice-fields of north-

western Eurasia and the enlarged alpine glaciers to the south united to obliterate the older plants of the continent, the Iberian tableland held its own. Obviously its 800 endemics, including many geographically segregated genera and others related only to groups of the most remote regions of the globe, are as ancient as any plants of Europe. But Atlantic Europe to the north, invaded by sea and ice, has "few endemics." This is precisely what one would expect, not because the flora of Atlantic Europe to the



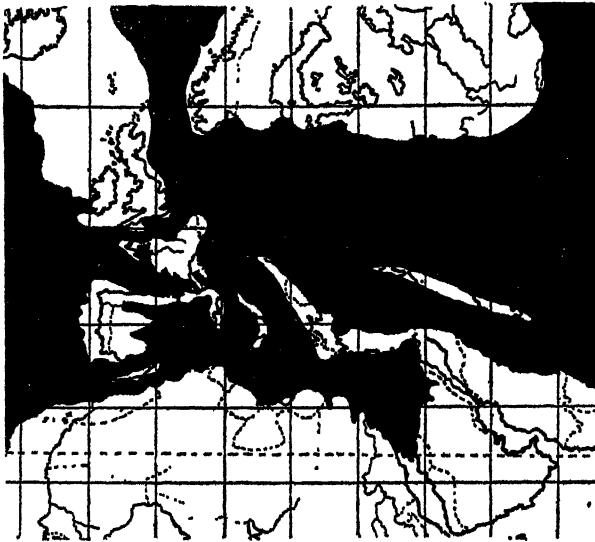
MAP 7. EUROPE IN LATE CRETACEOUS TIME, AFTER GRABAU (40, p. 805)

north is old, but because it is so very young.

The endemics of Japan, China, Mongolia and the Iberian peninsula have certainly had time to spread, but they behave exactly like the ancient endemics (epibiotics) of other regions. They are quite comparable with the species now confined to arctic Norway, arctic Russia, and Nova Zembla in Europe, north of the area invaded by the later advances of the European ice-sheets, and in North America found likewise only outside the areas which were

denuded by the later advances of the ice. These older species in America "have long since passed their period of aggressiveness. Left undisturbed they persist in their old habitats, but they fail to move into new and immediately neighboring territory." Similarly "in Scandinavia, where the de-glaciated Scandinavian alps offer most attractive habitats for them, they have rarely ventured out of the limited areas in which they were held trapped through the whole of Pleistocene time" (33, pp. 244, 246).

uniflora. As a general rule the late Mesozoic and early Cenozoic types, which have lingered in southeastern Asia and in southeastern North America, have quite disappeared from the Pacific slope of America; but, in case of the Indian Pipe, Nature, far from exterminating it, has allowed it to become a common woodland plant throughout eastern America and from Japan and Corea to the Himalayas, and she has even allowed it to remain on the Pacific slope, in Washington, Oregon, and California. Whiteness in saprophytic



MAP 8. EUROPE IN EOCENE TIME, AFTER GRABAU (40, p. 811)

Further arguing that endemics are young beginners which have not yet had time to spread, Willis cites the case of *Christisonia albida*, a saprophytic angiosperm of Ceylon, which was exterminated by its discoverer; and in extenuation of that catastrophe he adds: "it is probable that the white colour alone would have been such a disadvantage as to ensure its extermination by nature in any event" (91, p. 151). Nature, then, has wholly neglected her duty with the ghost-white Indian Pipe or Corpse Plant, *Monotropa*

angiosperms is unusual but it is not necessarily fatal, and in saprophytic agarics it is common. It is surmised that the extinction of *Christisonia albida* is readily explained by the destruction of the forests of Ceylon emphasized by Ridley (65, p. 559) and admitted by Willis (82, p. 191).

Finding that a large proportion of endemics in Ceylon were confined to solitary small areas on the mountain summits (just as in other mountainous regions), Willis, opposing the general interpretation that such species are survivors,

dramatically asked: "Had one arrived in Ceylon just in time to see the disappearance of a considerable flora?" To which Bateson promptly responded: "What more likely? Is the alternative interpretation, that he had come in time to attend the birth of a new flora, more acceptable?" (4, p. 42) and he further asked whether Willis really expects the local endemics of the bleak and arid mountain tops to leave those stations and spread over the tropical lowland. It is

these areas. There are more than 80 [after further exploration known to be 100] of these endemic species, plants with fundamental or deep-seated characters in their reproductive organs, all related to plants of British Columbia, Alberta, Washington, California, or Colorado and isolated by distances averaging 2000 miles from their nearest allies. Contrasted with this condition in Gaspé and western Newfoundland the situation in Atlantic western Nova Scotia is illuminating. There, in a region . . . which was denuded by the Pleistocene glaciers, the flora contains nearly 200 species which, after the receding of the glacial ice, made a landing off the coastal plain which has subsequently become



MAP 9. EUROPE IN MID-OLIGOCENE TIME, AFTER GRABAU (40, p. 812)

unlikely that the alpine endemics of Ceylon are really young beginners, and that their case is materially different from that of alpine endemics in many other regions.

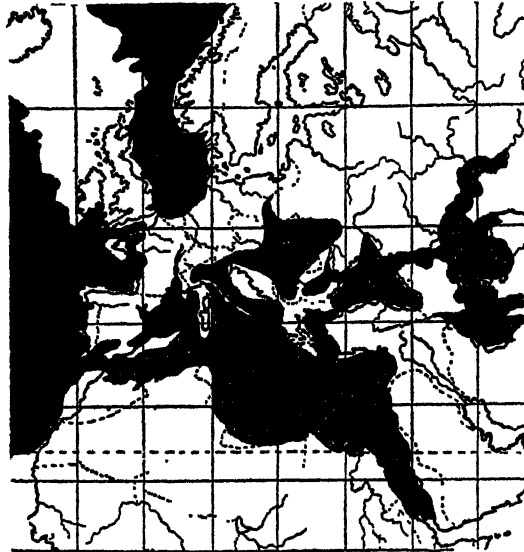
In my own studies in eastern America I have found that the unglaciated areas of Newfoundland and Gaspé are characterized by a large flora isolated from the West.

In connection with the occurrence in Gaspé and western Newfoundland of these hundreds of Cordilleran, Alaskan or Siberian species another point of great significance should be noted. This is the very large proportion of strictly endemic species found in

submerged and which now forms the continental shelf or banks off Nova Scotia. These are all plants derived from the southern coastal plain, some of them unknown nearer than the Pine Barrens of New Jersey, one at least unknown nearer than the Carolinas, and nearly all characteristic of the sandy coastal strip from southern New Jersey to Florida and Mississippi, there occurring in a climate obviously much warmer than that of the foggy coast from Digby and Yarmouth Counties to Guysborough, Nova Scotia. Yet in the 25,000 years (more or less) since this flora of far-southern origin became isolated on the Atlantic slope of Nova Scotia it has set off only a single endemic species and that a rapidly reproducing annual, the specific validity of which has been doubted. Otherwise the most Nature has accomplished in Nova Scotia toward segregation

from the southern types is the slight increase of hairiness or the modification of stature or foliage in about a dozen species. If we reason that the more thoroughly differentiated species, those with deep-seated differences in flower and fruit, are older than those which show only slight departures from type, then surely the floras of Gaspé and western Newfoundland, with their 80 [now known to be 100] endemic species mostly unrelated to any plants known nearer than about 2000 miles due west, are vastly older than the flora of Atlantic Nova Scotia (33, p. 242).

or Cenozoic time until this propitious moment, when the whole bunch is thrown off at once? In their occupation of very recently disturbed areas, *Rubus* and *Crataegus* are quite comparable with introduced weeds. When Willis's attention was called to the obvious fact that the behavior of the introduced weeds (like the common dandelion, the Canada Thistle, white-weed, burdock, Sheep Sor-



MAP 10. EUROPE IN PLIOCENE TIME, AFTER GRÄBAU (40, p. 819)

BEHAVIOR IN YOUTHFUL HABITATS

Turning to another angle of the question, if species are "thrown off" in regular mathematical progression through time, as Willis and Yule (93, 94, 95) maintain, how shall we explain the 500-600 (perhaps more) young beginners in *Crataegus* which have sprung up in the last three centuries "on the derelict farms of the Eastern States" (4, p. 42) and adjacent Canada? Have these and the equally modern host of Brambles or Blackberries (*Rubus* § *Eubatus*) simply been accumulating a large credit by withholding their "mutations" since Mesozoic

rel, etc., which in two or three centuries have completely covered the breadth of North America) absolutely disproved Age and Area, in that these are the youngest occupants of a country, not the oldest, he at once altered his definition to exclude introduced plants. But he has not ruled out the New Zealand "Veronics." In fact, he is very fond of citing them as proof of one point or another in his hypothesis.

Of this group, *Hebe*, in New Zealand Cheeseman says: "*Veronica* presents great difficulties to the systematist. Many of the species are singularly protean . . . varying so much . . . that it is no

easy matter to fix their real limits. Intermediate forms are numerous, connecting species that would otherwise appear most distinct, and . . . these intermediates blend so freely into one another that an apparently continuous series of forms is produced, while several species hybridize so readily in cultivation that the supposition at once arises that natural hybrids may also occur" (16, p. 491). Cockayne, likewise, emphasizes the lack of sharp specific lines in *Hebe* and adds: "Were . . . that school of botany which is dealing with *Rosa*, *Rubus*, *Hieracium*, and *Crataegus* in the Northern Hemisphere to study the New Zealand forms, several hundreds of species would be forthwith 'created'" (19, p. 44). He might have added *Panicum*, subgenus *Dichanthelium* (the "dichotomum group") which multiplies its segregates in the clearings and cranberry bogs of the Tertiary and Quaternary sands of eastern America, *Aster* § *Vulgares* of our swampy clearings and prairies, and many other groups.

Willis repeatedly refers to the fact that, although it is legitimate to consider many groups of endemic or near-endemic occurrence as relics of pre-existing floras "especially in the north temperate zone (particularly North America and China, [see map 6]) where the influence of the last glacial period was severely felt" (91, p. 88), "It would be absurd to apply the 'relic' explanation to such a case as . . . *Ranunculus* in New Zealand, and yet on this supposition *Ranunculus* in that country, or at any rate *Veronica* [meaning *Hebe*], must be considered as a relic" (91, p. 94). As already pointed out, there is every probability that *Hebe* is a relic, since its range today is almost exactly coincident with the present ranges of such genera as *Nothofagus* and *Araucaria*, both of which are relics of formerly wide-ranging groups.

As shown by the statements of ranges in New Zealand given by Cheeseman, 73 per cent of the species of *Hebe* are confined to the South Island (or sometimes to Chatham I. or Stewart I. to the south) and 17 per cent are on both the South and the North Islands; but only 10 per cent are confined to the North Island. In regard to *Ranunculus* Cheeseman states: "In New Zealand it forms a very conspicuous portion of the mountain vegetation, especially in the South Island . . . Many of them are exceedingly variable and difficult of discrimination. . . . Of the 37 species known, . . . 31 are endemic" (16, p. 7); and it is notable that the "difficult" species are exclusively among the endemics.

Now, so far as I can see *Hebe* and *Ranunculus* in New Zealand are misbehaving, like *Crataegus*, *Rubus* § *Eubatus*, *Hieracium*, the dichotomous *Panicums*, and numerous other groups in the northern hemisphere, for the simple reason that these groups, often of ancient lineage, have suddenly had opened before them large areas of virgin territory ready for invasion, and in the rapid occupation of the new habitats the formerly isolated and well-behaved species have freely mingled, with the result that we now have an intricate maze of undifferentiated and freely intergradient plants. In fact, Bateson has already stated that, "No one familiar with genetical work would be disinclined to believe that the vast group of endemic shrubby *Veronicas* were co-derivatives from one or more crosses" (4, p. 42). This interpretation in *Rubus*, *Rosa*, *Crataegus*, etc. is familiar. That the South Island of New Zealand was severely and recently glaciated there can be no question. Here are the words of Geikie: "the existing glaciers of New Zealand are the descendents, so to speak, of far greater ice-flows, which reached the

plains and may even have entered the sea. . . . The positions occupied by the terminal moraines show that the old glaciers were of very considerable importance after these moraines were deposited, the glaciers appear to have retreated continuously, and perhaps somewhat rapidly, as no terminal moraines are again met with, except in the immediate neighbourhood of the existing ice-streams. . . . In the south island of New Zealand we find a close analogy to the conditions that obtain in Scandinavia and Scotland" (37, pp. 717-719). It is, therefore, highly significant to find that ancient *Ranunculus* and presumably ancient *Hebe* have revived their youth and are now multiplying their species on the recently glaciated area of southern New Zealand, just as the ancient genera, *Rubus*, *Crataegus*, etc. are doing in the most youthful soils of the northern hemisphere. How can Age and Area tell us that *Rubus*, *Crataegus*, *Quercus*, *Ranunculus* and many other rejuvenated genera (probably including *Hebe*) are as old as *Liriodendron*, *Sassafras* and *Hamamelis*? Yet they are undoubtedly quite as old. This simple fact, that some of the Mesozoic genera are now seemingly on the wane while others of equal antiquity have revived their youthful vigor and pioneering capacity, is sufficient wholly to discredit the notion that we can determine the age of a group merely by the area it covers or by the number of its species.

RANGES OF ENDEMICIS

The endemics just discussed are obviously very young indeed and except that Willis, himself, draws them into the discussion by emphasizing *Hebe* and the New Zealand species of *Ranunculus*, they might be ruled out, not only because they act like the introduced weeds, but because Willis claims that he restricts his

discussion to "Linnean species." In general, alpine endemics are of the latter class and in discussing these epibiotics of Eurasia and Willis's view that they are young beginners, Ridley says: "I do not clearly see why the Alpine plants of the high mountains of the Malay Peninsula and Ceylon have a tendency to the reduction of leaves, and their having a tendency to become eventually quite round, orbicular in fact, and in case of compound leaves, simple, a state of affairs which does not occur in any of the species of the same genus in the wet forests at the base of the mountains; but there cannot be a shadow of doubt that it is of importance to the plant, and that the plants have been gradually adapted to their surroundings" (65, p. 565). And after discussing other cases in Ceylon and showing that Willis does not know the plants and their habitats but simply makes mechanical compilations, Ridley continues: "I confess I do not understand Dr. Willis's interpretation of the simple facts of evolution of a species as generally understood by naturalists. He states that the idea that endemic species were evolved to suit local conditions is based largely upon Wallace. Who ever possessed such a curious idea? Let us take some examples of endemics. *Aphyllanthus monspeliensis* is a liliaceous plant occurring in a limited area on the Mediterranean where it is distinctly endemic, a monotypic genus of the Sowerbieae section with no relations nearer than Australia. *Helxine Solerolii*, Req. (Urticaceae), is an endemic of Corsica and Sardinia and has no relations at all in this region. *Dioscorea pyrenaica*, Bub., is endemic to the Pyrenees and the only species of its genus in Europe. How could these plants be evolved to suit local conditions, unless they are the relics of floras of which the rest is extinct? There is nothing within

thousands of miles of them now from which they could be evolved. In cases like this, and there are very many, his mutation theory utterly collapses" (65, pp. 568, 569).

Willis's rhetorical query, in regard to the endemics of the Ceylonese mountains has been noted. In that case the plants were obviously relics. He makes a similar query in regard to *Senecio*. "It is very hard to suppose that a genus would choose certain spots upon the globe where its species should die out in large numbers, yet the facts of distribution require that this should be so under this explanation. Why should the *Senecios* retire to die, in large numbers, to Mexico, California, Bolivia, Peru, South Africa, Australia, etc.?" (91, p. 89). Who but Willis ever suggested that *Senecio* as a genus is dying out? As we have seen, following Small, he originates the genus in the northern Andes many millions of years before the high Andes of today existed. There the genus has phenomenal development and is a *mature* rather than a *dying* group. The monographer of the group, Greenman, finds that "There has been a relatively rapid northward migration of species . . . as far north as east-central Mexico and Cuba;" that there is "greater stability in morphological characters of the species occupying large areas as compared with the species occupying small areas—thus according in general with the age-and-area hypothesis;" but that "The origin of the respective species in the groups of plants specially considered appears *not* to have been through mutation of large size only, as held by Willis for the 'endemics' of Ceylon and New Zealand, but rather through natural selection in the course of a relatively rapid northward migration" (41, p. 193). In other words, *Senecio* in the mountains of tropical

America has not "retired to die" but is in the most active stage of maturity, not, as Small and Willis think, because it originated in the Cretaceous but because it is in a region geologically young. In the Andes and Mexico it is doing exactly what *Hieracium*, *Centaurea*, *Dianthus*, *Astragalus*, *Artemisia*, *Eriogonum*, *Hebe* and numberless other overwhelmingly large genera are doing in relatively youthful country in other parts of the world, certainly not "retiring to die."

Again Willis says: "The comparative rarity of seriously broken areas of distribution among endemic forms, especially south of the influence of the last glacial period, is much against any very large amount of dying out. One would not expect a moribund species to retain its area intact—though it is true that with the Cycads, often supposed moribund, this is largely the case" (91, p. 89). The Cycads are certainly more than "supposed moribund;" but, in regard to the general proposition, it is difficult to visualize a plant or animal having "seriously broken areas of distribution" and at the same time being "endemic;" and, in view of the recent glaciation of southern South America, southeastern Australia and Tasmania and southern New Zealand, it is likewise difficult to visualize any extensive flora and fauna "south of the influence of the last glacial period." Since Willis repeatedly states that, although Age and Area may break down in the North, but is the general rule in the region "south of the influence of the last glacial period," we are inclined to agree that it may be; the flora and fauna of the Antarctic ice-field may follow it! As to the "endemics" with "seriously broken areas of distribution," it may be possible that Willis is here adopting his recent redefinition of an endemic: "On larger areas of ground the proportions are

greater; Brazil has about 21 per cent of its genera endemic, and so has Chile, Australia about 30 per cent, . . . and the proportions increase with increasing area till one finds 100 per cent endemic in the World" (91, p. 170). In this larger area, where 100 per cent of the plants and animals occur (assuming that there are none in other worlds), there are so many groups (families, genera or species) with "seriously broken areas of distribution" that their detailed enumeration would nearly occupy the space of this article. Sufficient illustrations of them have already been given.

DISPERSAL OF SPECIES NOT CENTRIFUGAL

In regard to Willis's idea that plants originate at a center and then spread like concentric rings, it is obvious that he is dealing again with his imaginary world. Many botanists, Mrs. Arber, Sinnott and others, have discussed the theoretical objections and Schonland says: "the crux of Willis's 'Age and Area theory' consists in the assumption, that the dispersal of a species and of the new species derived from it must be centrifugal. Theoretically this may be conceded at the start, but by no means for all time to come" (68, p. 469). And Rendle remarks: "we cannot but hope that after all this is not the conclusion of the whole matter. If species originate by mutation and evolution and distribution are purely mechanical processes, what more is to be done?" (64, p. 307). This idea, that plants, after they have once got a start, *radiate* from a center, although erroneous, is common. For instance, such an idea in regard to our Arbor Vitae or White Cedar, *Thuja occidentalis*, whose ancestors date back to the Mesozoic, was recently put forward. Of this notion I wrote: "Hutchinson says . . . 'The northern area of its distribution is roughly outlined

by a semicircle, a fact which contributes evidence that *Thuja* has migrated radiately from a limited area . . . it does not migrate rapidly . . . this form has lagged behind.' When, therefore, following Hutchinson's suggestion, we draw the circle connecting the 'outliers' . . . it is impressive to find that the center of the circle falls in the great acid Archaean area northeast of Lake Superior, the Temagami region; for Hutchinson particularly informs us that 'it is notable that throughout great areas, for instance the Temagami region, *Thuja* is unknown.' And since the Temagami region was not accessible to forests until the vanishing of the Pleistocene ice, by Hutchinson's interpretation that the tree has 'migrated radiately' we are forced to the dramatic picture of the infant *Thuja occidentalis* created in very modern times in the center of the Temagami region and finding nothing to live on, migrating as rapidly as its 'lagging' tendency would allow to the calcareous regions northwest, north, east and south!" (30, p. 64).

Surely every botanist with the slightest experience in the field knows that in general plants do not spread radiately over large geographic areas. They follow belts of special soils, humidity or temperature and, with a great diversity of individual ecological or physiological requirements, each works out its range, which is anything but mathematically regular. Plants and animals in their dispersal are opportunists; their ranges are essentially all different and cannot be reduced to simple geometric patterns.

LIGNEOUS AND HERBACEOUS ALLIES

With *Hebe* of New Zealand still in mind let us look at Willis's reasoning about it (as "*Veronica*" in New Zealand). Arguing that ligneous groups are in general older than herbs, he says: "Only

very rarely, again, will one find a group of ten allied herbs, with a group of ten allied trees closely related to it. In such a case, which will very seldom occur, comparisons on the basis of age will be impossible" (91, p. 86); and again, "No one would suggest that a herbaceous genus of 100 species was of the same age as a tree genus with 100" (91, p. 116). Surely, *Hebe* (which, as we have seen, Cockayne believes to have hundreds of species equivalent in degree of segregation with those of *Crataegus*, *Rubus* and *Hieracium*) is closely related to the herbaceous genus *Veronica* (or the subgenus *Euveronica*). It consists of shrubs and trees and certainly Willis, by inference at least, derives them from the herbaceous genus of the northern hemisphere: "great ranges of mountains have sprung up . . . it is clear that they have completely altered the distribution of species . . . though on the other hand, species, chiefly herbaceous, which can live at high levels in the mountains, have been enabled to travel through and into regions otherwise impassable. It is in this way, probably, that many herbaceous and shrubby types of vegetation, including . . . *Veronica*, characteristic of the north temperate regions, but now also found in New Zealand, South America, etc., have been enabled to reach these countries" (91, p. 40). Willis merely infers the derivation of *Hebe* from the herbaceous *Veronicas*, but Cockayne gets beyond inference, saying in his paper, *Evolution of the Genus Veronica in New Zealand* (19, p. 44): "There is every evidence, then, of descent from a common ancestor, which, considering the genus beyond New Zealand as well as within its confines, would probably be an herbaceous plant with a didynamous capsule, such as *V. Chamaedrys* L." As I have already indicated, however, Pennell finds good reason to consider *Hebe* more

primitive than *Veronica*. This does not necessarily mean that all living woody genera, subgenera and species are older than their herbaceous allies. We know too many herbaceous types which are presumably of Mesozoic origin to believe that; and in the youthful flora of the cordilleran region of tropical America (mostly of Pliocene, Pleistocene or later origin) there are many ligneous members of groups which in older floras are represented only by herbs. The Morning Glories, *Ipomaea*, for instance, in the ancient floras of Australia and South Africa are herbaceous or at most suffrutescent or woody climbers, but in the region from western Mexico to Peru there occur numerous large trees (*Ipomaea* § *Arborescentes*); or *Oxalis*, which in South Africa is a large genus of geophilous herbs, in the youthful region from Mexico into the Andes has many ligneous representatives.

THE "HOLLOW CURVE"

One other point remains to be considered: Willis's "hollow curve." This Willis lays great stress upon, but the very definite fact, that competent mathematicians differ radically in their evaluation of it, is sufficient indication that, until its status is cleared, it is not an implement for the average botanist or zoölogist who deals with thousands of organisms, each with an independent life-history and geographic range. Willis, vigorously supported by Yule, finds the "hollow curve" the one correct representation of the facts of dispersal and evolution, but many others who have investigated it find it useless. Regan's flat statement that Age and Area "has no value" was based on a study of the "hollow curve" in which he showed that the same curve could be derived from a tabulation of the "names in a directory according to the

number of times each appears, etc., etc. . . . In other words the curve is not due to a single factor" (62, p. 165). Pantin, by making legitimate assumptions different from those of Willis, "came to conclusions directly opposite to those of Dr. Willis" and found that "we have in his curves direct evidence that:—(1) Evolution has proceeded almost entirely by natural selection (2) it is impossible to conceive of evolution proceeding by the large mutations suggested by Dr. Willis" (58). Newton, likewise, taking the same data as Willis, concluded: "It is now possible to deduce the converse of Dr. Willis's theorem" (57); and Chamberlain, after many tests of the work of "lumpers" and of "splitters" and with the crudest work and the best of monographs, concluded that "only in the most general sense will the quality of the data effect the form of the curve" (14, p. 308). With the mathematicians in complete disagreement as to the value of the "hollow curve" as a measure of evolution, the student of distribution can safely let it alone.

CONCLUSION

In this study I have purposely omitted any detailed discussion of the method of origin of species, since we are dealing with the dispersal not the origin of the organisms. I have also been obliged to omit practically all reference to the standpoint of the morphologist, the genetecist and the ecologist, since, with limited time for preparation, it has been necessary to keep pretty closely to the fields of classification and geographic distribution, which are most intimately concerned. In such discussions by the morphologist, genetecist and ecologist as I have come across there is no indication of approval of Age and Area; and, except for the applause of de Vries, the subject

south of the English Channel. Only the mathematicians and the philosophers see value in it and that is natural enough. It is an attractive concept and to those who do not realize the gross errors of fact involved, it seems very reasonable. Its only generally accepted proposition, however, is a truism which is not new. If the world were static it would be the obvious law. The world not being static, life has followed an intricate and almost inextricable series of factors, each acting differently on different species, with the result that no single factor, and especially *age*, can be isolated as all-controlling. Willis, as I have tried to show, has proceeded "without a full appreciation of the axiomatic truth that a work on phyto-geography should be based on a clear understanding of identities and of the geographic ranges of plants" (29, p. 215). "There is no branch of the botanical field which so much as phytogeography demands thorough training in exact taxonomic detail accompanied by the most discriminating judgment and prolonged and painstaking field-study" (29, p. 214); these Dr. Willis too obviously lacks. He has reared a superstructure with many attractive features but, unfortunately, he has neglected to consult frequently enough the taxonomists, the "hodmen of science" (see 52) and their co-workers in paleontology, geology, morphology and ecology, who control the brick and mortar necessary for the foundation. Without the secure foundation, which they in coöperation have to supply, the superstructure must necessarily collapse. "Age and Area" in 1915 was a "law;" by 1917 it had become "a hypothesis" and on the last page of his book, in 1922, Willis stated that it was "simply a corollary." By the mathematical rule which Willis believes to control all evolution, its status in 1926 could readily have

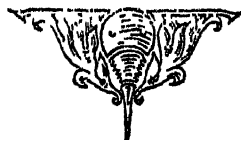
LITERATURE CITED

This bibliography, concerning so large a field, does not profess to be complete, and from the necessity of preparing this paper during a short vacation I have been forced to restrict it largely to the immediate fields of systematic and geographic botany and I have scarcely entered the fields of paleontology, morphology, ecology, genetics, etc., in their relation to Age and Area. It has seemed unnecessary to repeat most of the references published by Willis, but rather to supplement his bibliography.

- (1) ANDREWS, J. The age and area hypothesis. *Nature*, cxi, 114, 115 (1923).
- (2) ANTEVS, ERNST. The Recession of the Last Ice Sheet in New England (1922).
- (3) ARDER, AGNES. On the law of age and area, in relation to the extinction of species. *Ann. Bot.*, xxxiii, 211-213 (1919).
- (4) BATESON, W. Area of distribution as a measure of evolutionary age. *Nature*, cxi, 39-43 (1923).
- (5) BERRY, EDWARD W. A note on the age and area hypothesis. *Science*, xlii, 539, 540 (1917).
- (6) ———. Tree Ancestors (1923).
- (7) ———. Age and area as viewed by the paleontologist. *Am. Journ. Bot.*, xi, 547-557 (1924).
- (8) BEWS, J. W. Plant succession and plant distribution in South Africa. *Ann. Bot.*, xxxiv, 287-297 (1920).
- (9) ———. Some general principles of plant distribution as illustrated by the South African flora. *Ann. Bot.*, xxxv, 1-36 (1921).
- (10) ———. The south-east African flora; its origin, migrations, and evolutionary tendencies. *Ann. Bot.*, xxxvi, 209-223 (1922).
- (11) BOOTT, FRANCIS. Illustrations of the Genus *Carex*. 4 vols. (1858-1867).
- (12) BURTT-DAVY, JOSEPH. The distribution and origin of *Salix* in South Africa. *Journ. of Ecol.*, x, 62-86 (1922).
- (13) CALVERT, PHILIP P. The geographical distribution of insects and the age and area hypothesis of Dr. J. C. Willis. *Am. Nat.*, lvi, 218-229 (1923).
- (14) CHAMBERLAIN, JOSEPH CONRAD. Concerning the hollow curve of distribution. *Am. Nat.*, lviii, 350-374 (1924).
- (15) CHAMBERLAIN, T. C. AND SALISBURY, R. D. *Earth History*, vol. iii, (1906).
- (16) CHEESEMAN, T. F. *Manual of the New Zealand Flora* (1906).
- (17) CLARK, HUBERT LYMAN. Age and area and natural selection. *Nature*, cxi, 150 (1923).
- (18) CLARKE, C. B. On *Hemicarx*, Benth., and its allies. *Journ. Linn. Soc. (Bot.)*, xx, 374-403 (1884).
- (19) COCKAYNE, L. Observations concerning evolution, derived from ecological studies in New Zealand. *Trans. N. Z. Inst.*, xlv, 1-50 (1912).
- (20) ———. The Distribution of the Vegetation and Flora of New Zealand:—Cawthron Lecture, 1919 (1921).
- (21) COCKERELL, T. D. A. A fossil buttercup. *Nature*, cix, 42 (1922).
- (22) CUNNINGHAM, J. T. Origin of species and origin of adaptations [Abstract]. *Brit. Assoc. Adv. Sci. Rep. 19th Meeting (Hull-1922)*, 399, 400 (1923).
- (23) ———. Age and area and natural selection. *Nature*, cxi, 287 (1923).
- (24) DAKIN, W. J. The present position of Darwinism [Abstract]. *Nature*, cx, 753 (1922).
- (25) DE VRIES, H. The relative age of endemic species. *Science*, xlvii, 629 (1918).
- (26) DIXON, H. H. The present position of Darwinism [Abstract]. *Nature*, cx, 753 (1922).
- (27) DUNN, E. R. The geographic distribution of amphibians. *Am. Nat.*, lvii, 129-136 (1923).
- (28) FERNALD, M. L. A botanical expedition to Newfoundland and southern Labrador. *Rhodora*, xiii, 109-162 (1911).
- (29) ———. Harshberger's Phytogeographic Survey of North America. *Rhodora*, xiii, 213-224 (1911).
- (30) ———. Lithological factors limiting the ranges of *Pinus Banksiana* and *Thuja occidentalis*. *Rhodora*, xxi, 41-67 (1919).
- (31) ———. The Gray Herbarium expedition to Nova Scotia, 1920. *Rhodora*, xxiii, (1921).
- (32) ———. Isolation and endemism in north-eastern America and their relation to the age-and-area hypothesis. *Am. Journ. Bot.*, xi, 558-572 (1924).
- (33) ———. Persistence of plants in unglaciated areas of boreal America. *Mem. Am. Acad.*, xv, no. iii, 239-342 (1925).
- (34) FERNALD, M. L. AND WIEGAND, K. M. A summer's botanizing in eastern Maine and western New Brunswick, Pt. II. *Rhodora*, xii, 133-146 (1910).
- (35) GARDINER, J. STANLEY. The present position of Darwinism [Abstract]. *Nature*, cx, 753 (1922).

- (36) GATES, R. RUGGLES. The present position of Darwinism [Abstract]. *Nature*, cx, 753 (1922).
- (37) GRIBBS, JAMES. The Great Ice Age, ed. 3 (1895).
- (38) GLEASON, H. A. Evolution and geographical distribution of the genus *Vernonia* in North America. *Am. Journ. Bot.*, x, 187-202 (1923).
- (39) ———. Age and area from the viewpoint of phytogeography. *Am. Journ. Bot.*, xi, 541-546 (1924).
- (40) GRABAU, AMADEUS W. A Textbook of Geology, —Pt. II. Historical Geology (1922).
- (41) GREENMAN, J. M. The age-and-area hypothesis with special reference to the flora of Tropical America. *Am. Journ. Bot.*, xii, 189-193 (1925).
- (42) GUPPY, H. B. Fossil botany in the western world: an appreciation. *Am. Journ. Sci.*, xlix, 372-374 (1920).
- (43) ———. America's contribution to the story of the plant world. *Journ. Ecol.*, ix, 90-94 (1921).
- (44) ———. The testimony of the endemic species of the Canary Islands in favour of the age and area theory of Dr. Willis. *Ann. Bot.*, xxxv, 513-521 (1921).
- (45) HOLM, THEODOR. *Carex fraseri* Andrews, a morphological and anatomical study. *Am. Journ. Sci.*, ser. 4, iii, 121-128 (1897).
- (46) HOLMES, S. J. "Age and area" in relation to extinction. *Science*, lxi, 77-79 (1925).
- (47) HOOKER, J. D. Flora of New Zealand (1853).
- (48) HOUGH, ROMEYN BECK. Handbook of the Trees of the Northern States and Canada (1907).
- (49) HUXLEY, JULIAN. The present position of Darwinism [Abstract]. *Nature*, cx, 753 (1922).
- (50) JOHNSON, DOUGLAS. The New England-Acadian Shoreline (1925).
- (51) JOHANSEN, W. The present position of Darwinism [Abstract]. *Nature*, cx, 752 (1922).
- (52) JORDON, DAVID STARR. Hodmen of science. *Science*, lxii, 425, 426 (1925).
- (53) KÜKENTHAL, GEORG. Cyperaceae-Caricoideae in ENGLER, A. *Das Pflanzenreich*, iv²⁰ (1909).
- (54) LYELL, CHARLES. Principles of Geology, ed. 9 (1853).
- (55) MACKENZIE, K. K. *Carex* in BRITTON, N. L. AND BROWN, ADDISON. Illustrated Flora, ed. 2, i, 352-441 (1913).
- (56) MITCHELL, CHALMERS. The present position of Darwinism [Abstract]. *Nature*, cx, 752 (1922).
- (57) NEWTON, W. C. F. Age and area in biology. *Nature*, cxi, 48 (1923).
- (58) PANTIN, C. F. A. Statistical studies in evolution. *Nature*, cix, 273, 274 and 413 (1922).
- (59) PENNELL, FRANCIS W. "Veronica" in North and South America. *Rhodora*, xxiii, 1-22, 29-41 (1921).
- (60) POULTON, E. B. The present position of Darwinism [Abstract]. *Nature*, cx, 752 (1922).
- (61) PRAGER, R. LLOYD. Dispersal and distribution. *Journ. of Ecol.*, xi, 114-123 (1923).
- (62) REGAN, C. TATE. The present position of Darwinism. *Ann. Mag. Nat. Hist.*, ser. 9, xii, 164-167 (1923).
- (63) RENDLE, A. B. The present position of Darwinism [Abstract]. *Nature*, cx, 753 (1922).
- (64) ———. Age and Area [Review]. *Journ. Bot.*, lx, 306, 307 (1922).
- (65) RIDLEY, H. N. On endemism and the mutation theory. *Ann. Bot.*, xxx, 551-574 (1916).
- (66) ———. The distribution of plants. *Ann. Bot.*, xxx, 1-29 (1923).
- (67) ———. Endemic plants. *Journ. Bot.*, lxiii, 182, 183 (1925).
- (68) SCHONLAND, S. On the theory of "age and area." *Ann. Bot.*, xxxviii, 453-472 (1924).
- (69) SCHUCHERT, CHARLES. Historical Geology (1915).
- (70) SEWARD, A. C. The present position of Darwinism [Abstract]. *Nature*, cx, 753 (1922).
- (71) SINNOTT, EDMUND W. The "age and area" hypothesis and the problem of endemism. *Ann. Bot.*, xxxi, 209-216 (1917).
- (72) ———. The "age and area" hypothesis of Willis. *Science*, xlvi, 457-459 (1917).
- (73) ———. Age and area and the history of species. *Am. Journ. Bot.*, xi, 573-578 (1924).
- (74) TANSLEY, A. G. Review of HAGEDOORN, A. L. and HAGEDOORN, A. C.: The Relative Value of the Processes Causing Evolution. *New Phyt.*, xx, 124-131 (1921).
- (75) TAYLOR, NORMAN. Endemism in the flora of the vicinity of New York. *Torreya*, xvi, 18-27 (1916).
- (76) ———. Endemism in the Bahama flora. *Ann. Bot.*, xxxv, 523-532 (1921).
- (77) TRELBASS, WILLIAM. The American Oaks. *Mem. Nat. Acad. Sci.*, xx, (1924).
- (78) WAGNER, H. The present position of darwinism [Abstract]. *Nature*, cx, 752 (1922).

- (79) WILLIS, J. C. The endemic flora of Ceylon, with reference to geographical distribution and evolution in general. *Phil. Trans. Roy. Soc. Lond., Ser. B*, ccvi, 307-342 (1915).
- (80) ———. The evolution of species in Ceylon, with reference to the dying out of species. *Ann. Bot.*, xxx, 1-23 (1916).
- (81) ———. The distribution of species in New Zealand. *Ann. Bot.*, xxx, 437-457 (1916).
- (82) ———. The relative age of endemic species and other controversial points. *Ann. Bot.*, xxxi, 189-208 (1917).
- (83) ———. The distribution of the plants of the outlying islands of New Zealand. *Ann. Bot.*, xxxi, 327-333 (1917).
- (84) ———. Further evidence for age and area; its applicability to the ferns, etc. *Ann. Bot.*, xxxi, 335-349 (1917).
- (85) ———. The sources and distribution of the New Zealand flora, with a reply to criticism. *Ann. Bot.*, xxxii, 339-367 (1918).
- (86) ———. The flora of Stewart Island (New Zealand): a study in taxonomic distribution. *Ann. Bot.*, xxxiii, 23-46 (1919).
- (87) ———. The floras of the outlying islands of New Zealand and their distribution. *Ann. Bot.*, xxxiii, 267-293 (1919).
- (88) ———. On the floras of certain islets outlying from Stewart Island (New Zealand). *Ann. Bot.*, xxxiii, 479-484 (1919).
- (89) ———. Plant invasions of New Zealand with reference to Lord Howe, Norfolk, and the Kermadec Islands. *Ann. Bot.*, xxxiv, 471-492 (1920).
- (90) ———. Endemic genera of plants in their relation to others. *Ann. Bot.*, xxxv, 493-512 (1921).
- (91) ———. Age and Area, a Study in Geographical Distribution and Origin of Species, with Chapters by DE VRIES, HUGO, GUFFY, H. B., REID, MRS. E. M. AND SMALL, JAMES (1922).
- (92) ———. The inadequacy of the theory of natural selection as an explanation of the facts of geographical distribution and evolution [Abstract]. *Brit. Assoc. Adv. Sci. Rep. 19th Meeting (Hull—1922)*, 399 (1923).
- (93) WILLIS, J. C. AND YULE, G. UDNEY. Statistical studies in evolution. *Nature*, cix, 274, 413 (1922).
- (94) YULE, G. UDNEY. A mathematical conception of evolution based on the theory of age, size, and space [Abstract]. *Brit. Assoc. Adv. Sci. Rep. 19th Meeting (Hull—1922)*, 399 (1923).
- (95) ———. A mathematical theory of evolution based on the conclusions of Dr. J. C. Willis, F.R.S. *Phil. Trans. Roy. Soc. Lond., Ser. B*, ccxiii, 21-87 (1924).





HOST RESISTANCE AND TYPES OF INFECTIONS IN TRYPANOSOMIASIS AND MALARIA

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I. INTRODUCTION

CLASSICAL immunology has been chiefly concerned in the past with the host and not the parasite. It has attempted to study the properties of immune sera as opposed to normal sera and to correlate the former with the defense of the host against the invading parasite or to use the former in detecting the presence of a suspected parasite. In the present review the author wishes to shift this emphasis slightly by correlating the properties of immune sera with the activities of the parasite. By this approach to the subject it is hoped that some of the immunological bases for the different types of infection will be disclosed.

The difficulty of studying the subject from this aspect lies in the fact that in order to get at the activities of the parasite all the stages in its life-cycle must be localized in some accessible part of the host where they may be studied from day to day. Certain of the plasmodia and trypanosomes comply with this prerequisite since they complete their life-cycle in the general blood stream and can be found in the peripheral blood. They will, consequently, be taken up in detail, while others, unsuitable in this respect, will not be considered. Thus, *Trypanosoma cruzi*, which shows more similarities to the leishmanias than to the trypanosomes, is predominantly a

tissue parasite and can only rarely be found in the blood-stream. Likewise, *Halteridium* of birds and *Plasmodium falciparum* of man undergo their asexual life-cycles chiefly in the blood vessels of the deeper tissues.

For a detailed description of the parasites considered in this review and their relatives, the reader is referred to any of the standard texts on protozoology, such as Hegner and Taliaferro (1924). Only the barest details can be given here. The genus *Trypanosoma* is very widely distributed, and species are found parasitic in the blood of various vertebrates belonging to almost every class. In the present paper a distinction is made between pathogenic and non-pathogenic or non-lethal forms. By far the majority of the known species belong to the second group and produce no observable symptoms in their hosts. A representative of this group is *T. lewisi*, the common blood parasite of rats all over the world. By pathogenic trypanosomes is generally meant those which produce disease in man or animals, such as, *T. gambiense* and *T. rhodesiense* of human sleeping sickness, *T. cruzi* of Chagas' disease, *T. brucei* of nagana of domestic animals, *T. equinum* of mal de caderas of horses and mules, and *T. equiperdum* of equine dourine. Even these forms which are generally lethal to man or domestic animals can probably live in certain wild animals without producing appreciable symp-

toms. Among the malarial parasites, *Plasmodium falciparum*, *P. malariae* and *P. vivax* of the malignant tertian, quartan and benign tertian fevers of man are too well-known to need discussion. In man, malaria, though often fatal, tends toward recovery. *P. relictum*, the bird parasite, is generally non-lethal.

Figure 1 gives some outline drawings of *Trypanosoma lewisi* taken (1) when the parasites are actively reproducing, (2) when actual cell division is rare, but when growth stages due to reproduction are still present and (3) when all reproduction has stopped. Although the pathogenic trypanosomes considered do not reach a stage, in laboratory animals, when all cell division ceases, their morphology differs from *T. lewisi* only in minor details. Figure 2 shows the intracellular bird malaria parasite (*Plasmodium relictum*) and indicates the 24-hour asexual cycle which occurs in this parasite.

A knowledge of the general course of infection of the trypanosomes and malarial organisms has gradually accumulated as a result of many types of experimental work. The author cannot, therefore, review progressively the steps in its compilation, but will, instead, outline the general facts in regard to these infections, and in passing, note a few specific pieces of work which seem particularly important. Moreover, to avoid repetition it has seemed best, first, to outline briefly the methods devised for determining the effects of the host's resistance on the parasite in the various types of infection, and second, to follow this with a consideration of each of the main types of trypanosome and malarial infections. These types of infections will in turn be discussed with regard to the following points: first, to review the course of the infection; second, to apply the methods of

analyzing the effects of resistance which will have been previously outlined; and third, to give the immunological bases

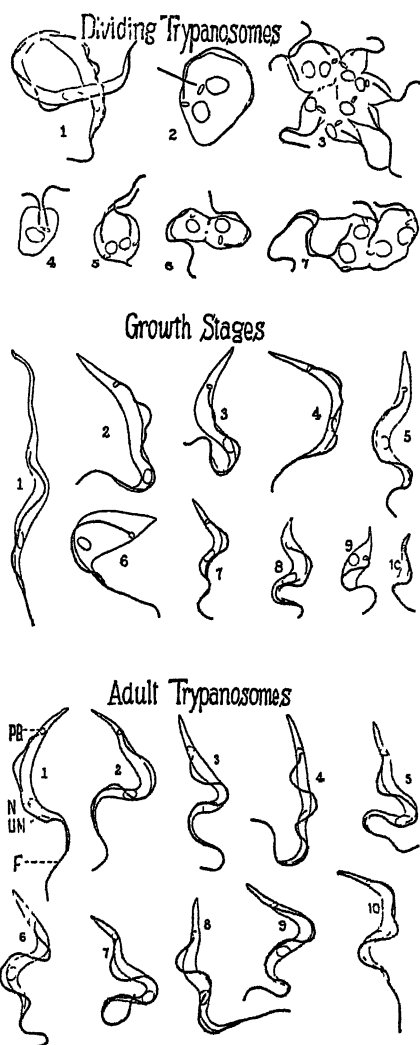


FIG. 1. *TRYPANOSOMA LEWISI*

1. Dividing trypanosomes such as are found at the height of reproductive activity. 2. Growth stages, taken from the fourth day of the infection shown in figure 5. 3. Adult forms, taken from the twenty-eighth day of the same infection. F, flagellum; N, nucleus, P. B., parabasal body; U. M., undulating membrane. $\times 1000$. (1, after Coventry; 2 and 3, after W. H. Taliaferro.)

for these effects in as far as they are known.

Before taking up the methods devised for determining the effects of the host's resistance on the parasite, the term resistance, itself, needs defining. Resistance, in the broad sense, may be used to

the body of the host adverse to the parasite; as efforts on the part of the body to make good the deleterious effects of the parasite as in the hyperactivity of the hematopoietic organs due to the destruc-

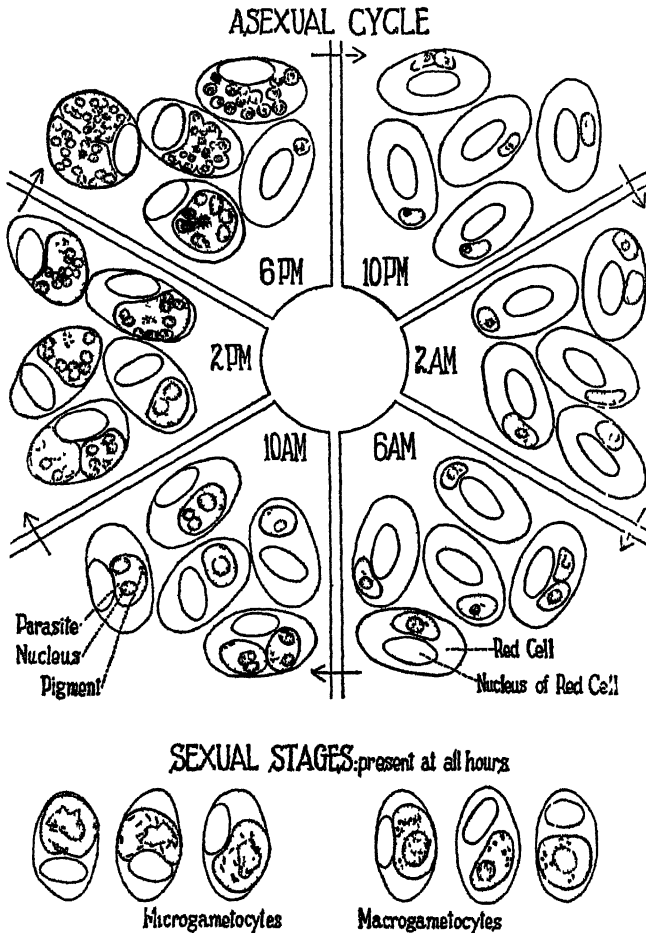


FIG. 2. REPRESENTATION OF THE CYCLE OF REPRODUCTION IN BIRD MALARIA SHOWING CHANGES IN SIZE AND VARIABILITY

Outlines of the asexual stages ($\times 1500$) of the parasites within the red cells, showing nuclei and pigment granules, made at four hour intervals during a consecutive period of 24 hours. In addition, outlines of three microgametocytes and three macrogametocytes, which occur in small numbers at all hours throughout the infection. (From drawings by L. G. Taliaferro.)

denote various mechanisms, either active or passive, of the host to counteract the activities of the invading parasite. It may be manifested as hindrances to the act of invasion; as conditions arising in

tion of red cells in malaria; or by the production of antitoxins in those infections where toxins are formed. Throughout this paper, however, the term resistance will be restricted, as a matter of con-

venience, to denote the various conditions arising in the host which are adverse to the parasite, since the author hopes to show later that the different types of infection may be directly correlated with the host's resistance in this sense. It is also to be noted that resistance in any sense may be either natural or acquired. Natural resistance is correlated with such matters as species immunity, etc., and although it undoubtedly plays some part in the types of infection, it may not be the result of infection. Acquired resistance, on the other hand, is developed after the parasite has successfully invaded the host, and, as will be shown later, is adequate to explain the broad differences in the various types of infection considered in this paper. The present review, therefore, will be limited to considerations of acquired resistance.

Acquired resistance, as just defined, is generally thought of as paralleling the production of immune antibodies or reaction products in the host. "As antibodies have never been isolated in a pure condition we have no knowledge as to what they are, and their existence is recognized merely by the effects they produce, just as we recognize the existence of enzymes" (Wells, 1925). Furthermore, although they may represent new material substances arising in the host as a result of infection or processes of immunization, they may just as well represent a change in substances already present or even a change in the concentration of such substances.

II. METHODS OF ANALYZING THE EFFECTS OF RESISTANCE

The methods devised for determining the effects of the host's resistance on the parasite in the various types of infection can now be outlined. Granted that a parasite not only has successfully in-

vaded its specific host but has started reproduction, it is evident that if no resistance is operative it must increase in the blood at a uniform rate. Also, due to the fission-method of protozoan reproduction, such an unmolested increase would cause it to accumulate according to a geometrical progression series (a , ar , ar^2 , ar^3 , ar^4 , ar^n , for example, 1, 2, 4, 8, 16, etc.). If it does not progress uniformly in this manner (and the majority of infections studied do not), for example, if after it has appeared in the host as an infection, its numbers either remain constant or decrease, we may conclude that some type of resistance is operative. In other words, in the number curves of different infections, we have an approximate method of ascertaining whether any resistance is operative and an approximate measure of the sum total effects of this resistance. Parenthetically, it may be noted that the rate of reproduction might *increase* due to a lowering of the natural resistance of the host, but with little experimental evidence indicating this, it is not considered.

Any fluctuations in the number curve, however, can be brought about by one or both of two entirely different mechanisms: 1, the rate of reproduction of the parasites (cell division) may be retarded or inhibited; or 2, the parasites may be destroyed after they are formed. The second mechanism includes those effects of resistance which may be termed *parasitocidal*, but the inhibition of reproduction may not be parasitocidal at all. Practically all discussions of the effects of resistance have hitherto been limited to the parasitocidal effects.

Although the general phenomenon of the cessation of reproduction in infections with *Trypanosoma lewisi* has been known for many years and the presence of cycles of reproduction in *T. gambiense*

since 1912 (Robertson, 1912), the sharp distinction between these two effects of resistance was probably first clearly brought out by the present author and L. G. Taliaferro (1922). The principle of inhibition of reproduction as an immune phenomenon is recognized by van Saceghem (1923) and definitely correlated with a property of immune serum by Taliaferro (1924). These investigations will later be considered in detail. As Taliaferro, W. H. and L. G. (1922) point out, the separate action of the reproduction inhibiting and the parasitocidal effects of resistance which collectively account for the number of organisms present in the blood at any time is clearly indicated in the following equation:

$$\left. \begin{array}{l} (1) \\ \text{Number of} \\ \text{parasites} \\ \text{at any} \\ \text{time} \end{array} \right\} = \left\{ \begin{array}{l} (2) \\ \text{Number pro-} \\ \text{duced by} \\ \text{reproduc-} \\ \text{tion} \end{array} \right\} - \left\{ \begin{array}{l} (3) \\ \text{Number} \\ \text{destroyed} \end{array} \right\}$$

Here the reproduction inhibiting effect directly affects the second member of the equation and the parasitocidal effect represents the third member. As the members of this equation can not be measured exactly it can not be solved in a mathematical sense. Nevertheless, fairly accurate conclusions can be drawn by the methods outlined in the next paragraphs.

In the work of Taliaferro, W. H. and L. G. (1922) and Taliaferro, W. H. (1924) on trypanosomes, and Taliaferro, L. G. (1925) on bird malaria, the first and second members of the equation have been determined and the third evaluated in the following manner. The first term can be easily obtained by making frequent parasite counts during the course of an infection. The second term of the equation (rate of reproduction), in order to be valid, must be independent of both the

first and third terms, and hence, can in no way depend on the enumeration of the progeny formed. A measure to fill these requirements has been found and although it is indirect, it can be used as long as there are enough parasites in the blood to furnish suitable samples for analysis. Since reproduction in malaria, however, proceeds in cycles, whereas in trypanosome infections it does not, a different method is used in the two groups.

In the trypanosome infections, the measure consists, essentially, in comparing the variability in size of samples of trypanosomes taken at stated intervals throughout the course of an infection. The rationale of this method is based on the obvious and well-known fact that a sample of organisms measured, on the one hand, from a population undergoing rapid reproduction, with the constant production of young forms and intermediate growth stages, will exhibit much greater variability in size than a sample of organisms measured, on the other hand, from a population in which there is little or no reproduction and in which all of the organisms are full-grown adults. (Compare, for example, the variations in length of the reproducing with the constancy in length of the non-reproducing parasites in figure 1.) Throughout the work, the total length of the trypanosomes was selected as the most suitable measure of size while their variability was expressed in terms of the coefficient of variation. This statistical constant was computed from the actual measurements by means of the usual formula and expresses the variability in terms of percentages of the mean size. In *T. lewisi*, for example, a coefficient of variation for total length of 3 per cent indicates a population of adults in which there is no reproduction and a coefficient of variation of 30 per cent indicates a population in

which reproduction is ensuing at a maximum rate.

The coefficient of variation method is applicable to trypanosome infections because in these the organisms reproduce by binary fission and do not exhibit any periodicity in reproduction. Thus, if reproduction is going on, a random sample at any time will give all stages of reproduction and growth. In the malarial parasites, however, the asexual forms sporulate and grow up nearly synchronously (cf. fig. 2). Thus, a sample at one time will contain only small forms (merozoites); at another, large forms (schizonts), etc. The length of time it takes for the organisms to complete this cycle of growth and sporulation is the time it takes for each small organism to grow up and produce about 15 progeny, and is, therefore, actually an expression of the rate of reproduction of parasites. Should this time vary anywhere during the infection, the rate of reproduction could accordingly be said to vary. It is to be noted that examinations of blood smears to ascertain when sporulation takes place would give a rough measure of the rate of reproduction. A more exact method, which was the one used, is as follows: 50 parasites were drawn, measured and their mean size obtained at 2- or 4-hour intervals during as much of the infection as was possible. As can be seen from figure 2, the data obtained showed a series of abrupt falls and gradual rises in the mean size of the parasites, due to the fact that when the parasites occurred in the blood as large schizonts, their mean size was high; when sporulation took place, their mean size immediately dropped, but gradually rose, as growth ensued, until the next period of sporulation. Comparing the time it takes for this cycle to be completed during the various stages of the infection (acute,

chronic and relapse) it can be ascertained whether the rate of reproduction is changing or being maintained constant. In one strain of bird malaria, for example, the cycle was found to take twenty-four hours whenever it was possible to obtain data, and therefore, the rate of reproduction can be considered as constant throughout the entire infection. This measure of the rate of reproduction supposes that the *average* number of young produced by each full-grown parasite at each sporulation period does not vary throughout the infection. This has been shown to be a valid assumption by L. G. Taliaferro (1925). Obviously, this method has the same advantage as the coefficient of variation method in the trypanosome infections in that it is independent of the number of parasites destroyed, and can be used as long as enough parasites remain in the blood to obtain a statistically valid sample.

III. CONTINUOUS INFECTIONS OF THE PATHOGENIC TRYPANOSOMES IN THE MOUSE

When most varieties of the pathogenic trypanosomes which produce disease in man and domestic animals are injected into mice, the parasites appear in the blood after a short incubation period and increase in numbers steadily and uniformly until the death of the host. This is the simplest type of infection met with. Much the same type of infection is seen in the rat. Sometimes, however, the parasites in this host temporarily disappear from the blood and the infection, consequently, more nearly approaches that seen when the pathogenic trypanosomes are grown in the guinea pig as described in the next section. The general nature of the infection in the mouse and its difference from that in the guinea pig was recognized by the earlier writers; for

example, it was clearly pointed out by Massaglia (1907).

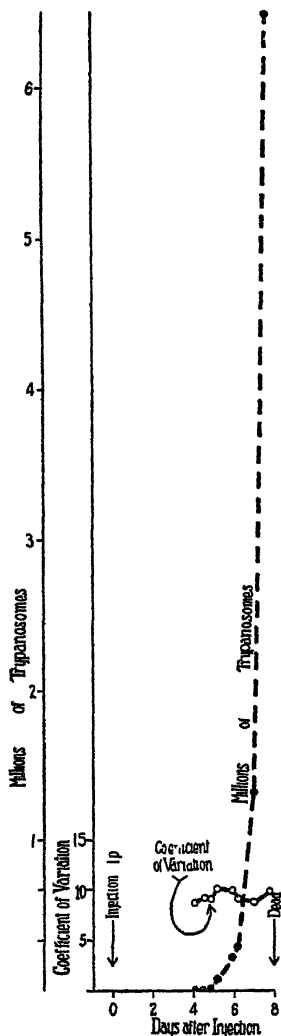


FIG. 3. GRAPH SHOWING THE COEFFICIENT OF VARIATION FOR TOTAL LENGTH (COMPARATIVE MEASURE OF THE RATE OF REPRODUCTION) AND THE NUMBER OF TRYPANOSOMES PER CUBIC MILLIMETER OF BLOOD, THROUGHOUT THE COURSE OF AN INFECTION WITH *T. RHODESIENSE* IN A MOUSE

This infection illustrates the condition in which there is neither any inhibition of reproduction of the parasites nor any appreciable parasitocidal action. (From data by W. H. and L. G. Taliaferro.)

T. rhodesiense, the causative agent of one type of human sleeping sickness, in

the mouse, taken from Taliaferro, W. H. and L. G. (1922), illustrates this type of infection. After an intraperitoneal injection of infected blood, the trypanosomes appeared in the blood 4 days later, and the mouse died 7 days after injection. (See fig. 3.) Blood smears were made every 12 hours while the organisms were in the blood. After staining and upon examination, they gave the results which are represented graphically in figure 3. (In the graphs of the trypanosome infections, i.e., figures 3, 4, 5, and 6, all of the data are represented on the same scale with the exception of the number curve in figure 3 which of necessity is considerably reduced. This makes possible a direct comparison of the different types of infection.) The variability of the parasites remained fairly high (C.V. = 8.87 to 10.46 per cent) throughout the infection with no indication of a progressive change in it—from which we may conclude that the rate of reproduction remained approximately the same throughout. Furthermore, microscopical examination of the slides showed that cell division of the parasites was occurring throughout the infection. The number of organisms in the blood steadily accumulated according to a geometrical progression which, as has been said before, is just what would be expected if none or very few of the organisms were being killed. Hence, we may conclude that no resistance whatever is acquired by the host, either affecting the rate of reproduction of the parasites or destroying them after they are formed.

IV. INFECTIONS WITH PATHOGENIC TRYPANOSOMES PROCEEDING BY CRISES AND RELAPSES

When the same pathogenic trypanosomes considered in Section III are grown in the guinea pig, the infection is charac-

terized by alternate increases and decreases in the number of parasites found in the blood (fig. 4). The periods of more or less sudden disappearance of the parasites from the blood are known as crises and the re-population of the blood following the crises as relapses. As has already been pointed out, the general nature of such infections has been well-known for a number of years. Fantham and Thomson (1911) applied exact enumerative methods throughout the course of infections of *T. rhodesiense* and *T. gambiense* in guinea pigs and rats, and Thomson (1912) has applied the same

of wholesale destruction of the parasites and not simply periods of temporary migration of the organisms from the blood stream. In analyzing the effects of the host's resistance to the organisms, therefore, it may be concluded from this early work that one effect of resistance in these infections is the destruction of large numbers of the parasites at certain intervals. Is this destruction associated with any effect on the rate of reproduction *per se*? Our work indicates that it is not. For example, the coefficient of variation for total length (Taliaferro, W. H. and L. G., 1922) of *T. rhodesiense* throughout an

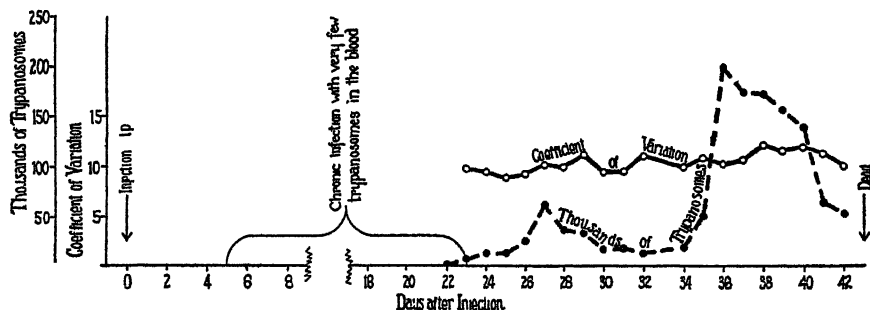


FIG. 4. GRAPH SHOWING THE COEFFICIENT OF VARIATION FOR TOTAL LENGTH (COMPARATIVE MEASURE OF THE RATE OF REPRODUCTION) AND THE NUMBER OF TRYPANOSOMES PER CUBIC MILLIMETER OF BLOOD, THROUGHOUT THE COURSE OF AN INFECTION WITH *T. RHODESIENSE* IN A GUINEA PIG

This infection illustrates the condition in which there is no inhibition of reproduction of the parasites, but in which there is a marked parasiticidal effect, as is shown by the first chronic stage of the infection and by the two well-marked number crises. (From data by W. H. and L. G. Taliaferro.)

methods to infections with *T. brucei* in the same hosts.

Besides the guinea pig, this kind of infection has been found in other hosts. Thus, it is quite often observed when the dog is infected with the pathogenic trypanosomes; it was found by Ross and Thomson (1910a) to be characteristic of infections of *T. rhodesiense* in man, and in the author's experience, generally occurs when *T. equinum* is grown in rats.

The sudden disappearance of the parasites from the blood, coupled with the *in vitro* serological studies which we will review later, early convinced investigators that the crises were actual periods

entire infection in the guinea pig remains at the high level of 9 to 10 per cent (fig. 4). Essentially similar results are obtained in the dog. Here, as in the infections in the mice, direct microscopical examination of the slides showed that the parasites were undergoing cell division whenever they could be found. In other words, once the parasites are introduced into the host, they probably reproduce at a uniform rate during the entire infection. At intervals, however, most of the parasites that have accumulated in the blood are destroyed, but the few, which escape destruction, since their rate of reproduction is unchanged, repopulate

the blood again and again until the host dies. Expressed in terms of resistance, in this type of infection, which proceeds by crises and relapses, one of the two possible effects of resistance is operative, i.e., the host's resistance is directed toward a destruction of the parasites after they are formed but not toward an inhibition of the rate of reproduction *per se*.

What is the mechanism of this destruction? The available evidence indicates that at the crisis there is a sudden acquisition of a trypanolytic property by the blood serum and that the organisms accumulate in the blood during the relapse *not* because the lytic antibody disappears but because the trypanosomes are so changed biologically as to be no longer susceptible to the action of the antibody. These data have been obtained from two different lines of investigation: first, the study of the trypanocidal antibodies arising in animals as a result of the partial or complete cure of infections, and second, the study of the trypanolytic antibodies occurring during the uninfluenced course of experimental infections. Although it might be questioned whether the trypanocidal effects in these two classes of experiments are the same, they nevertheless point to the same conclusions.

It was recognized early in the experimental work with trypanosomiasis that the serum of some infected animals lysed the same species of trypanosome. This phenomenon was probably first noted by Schilling (1902) in a bull "immunized" against nagana (*T. rogersi*). Franke (1905) also noted it in an Old World monkey (*Cercopithecidae*) cured of mal de caderas (*T. equinum*). He also observed the very important fact, from the standpoint of the mechanism of relapse, that the blood of the infected monkey could contain simultaneously the trypanosomes and strong trypanocidal antibodies.

Evidently, these resistant organisms were different from the original passage strain, and he states, "dass die Parasiten andere biologische Eigenschaften angenommen haben und für die Schutzstoffe unempfindlich geworden sind." Lingard (1904) also noted that the serous fluid from the plaques of horses with dourine (*T. equiperdum*) was trypanolytic.

The study of the trypanocidal antibodies which arise following treatment and their relation to relapse antedates the work on the course of natural infections and will therefore be considered first. Beginning with the original work of Franke (1905), Ehrlich and his co-workers, Roehl, Gulbransen and Ritz, have carried out a very ingenious series of experiments on the mechanism of relapse in infections with the pathogenic trypanosomes in the mouse. As has already been pointed out, the uninfluenced infection in this host is of the continuous progressive type, and therefore, crises and relapses had to be produced by means of incomplete cures with drugs. With such artificially produced crises and relapses, they tested the identity or non-identity of their original and relapse strains by using a previous observation of Ehrlich and Shiga (1904), which was confirmed by Halberstaedter (1905) and Franke (1905), that if a mouse is cured of an infection with a pathogenic trypanosome, it is refractory for about 20 days to a second infection with the same strain. This immunity is so specific that it serves to differentiate between the original and the relapse strains. In this type of work it might be thought that the immunity after cure is due to the retention of the trypanocidal drug. Ehrlich and Shiga (1904) showed that this was not true but that it is connected with a specific immunological reaction on the part of the host. It has also been shown that par-

tial cure results in the production of similar specific antibodies.

An hypothetical experiment will serve to show how these experimenters differentiated original and relapse strains: A mouse is infected with a strain of trypanosomes which is called the *passage* or original strain. When the trypanosomes appear in the blood, a trypanocidal drug is given to the mouse in a dose sufficient to cause a temporary but not a permanent disappearance of the parasites from the blood. The parasites which reappear constitute a *relapse* strain. Before the drug treatment one set of mice is subinoculated from the passage strain, and after treatment another series is subinoculated from the relapse strain. Now, if one of the mice be cured of its infection with the passage strain, it is immune to subsequent reinjections of the same strain, but it becomes infected and dies if inoculated with the relapse strain. Similar experiments can be carried out with the relapse strain. Immunity, therefore, toward the passage strain does not protect against the relapse strain, and *vice versa*, showing that the two are biologically different. The fact that the relapse strain is actually different from the original strain has been demonstrated in this manner by Ehrlich (1909), Ehrlich, Roehl and Gulbransen (1909), Rosenthal (1913) and Ritz (1914).

Of the papers mentioned, the one of Ritz (1914) is of particular interest. One of his mice was incompletely cured 20 times with the production of 17 immunologically different relapse strains. Some of these strains were identical with those of another mouse which had been incompletely cured 19 times with the production of 9 immunologically different strains. Thus, when the relapse strains in each mouse were numbered consecutively he found that No. 7 of the first

mouse was the same as No. 3 of the second and Nos. 6, 9 and 8 of the first were the same as Nos. 4, 5 and 11 of the second, respectively. In over 600 mice he found 22 immunological variations.

Ehrlich, Roehl and Gulbransen (1909) and Ehrlich (1909) added another important contribution in that they found that trypanosomes could be made resistant *in vitro* to the trypanocidal antibodies which arise in mice after treatment. If mice were infected with the passage strain, cured, and then bled, their serum was found to be trypanocidal. If some of the original passage trypanosomes were now allowed to stand in contact with this serum for 15 minutes and then injected into normal mice, the trypanosomes from the resultant infection were found thereafter to be resistant to the trypanocidal serum. Furthermore, this resistance was retained for over a year, entailing over 200 passages through mice.

While these investigations were going on, other workers were studying the mechanism of relapse in uninfluenced infections where crises and relapses occurred naturally. The first systematic work on the lysins arising during the course of uninfluenced infections and their relation to crises and relapses was that of Rodet and Vallet (1906). Besides recognizing the lytic properties of the serum, these authors believe that certain organs, notably the spleen, have remarkable trypanolytic properties. Later work tends to show that this is not the case although Mutermilch (1911) has presented evidence that the trypanolysins are formed in the spleen and other hematopoietic organs. According to him, however, after these antibodies are thrown into the blood, the organs contain no more than can be accounted for by the blood in them. Similarly, certain authors have advanced evidence that phagocytosis

plays a significant part in the disappearance of the parasites, but from the literature, as well as from various unpublished experiments, the present author believes that such phagocytosis is a secondary phenomenon and that the trypanosomes which are phagocytosed have already been injured, if not killed, by agencies present in the serum.

Massaglia (1907) showed that a definite correlation existed between the crisis and the lytic property of the serum. Thus, in a guinea pig before the crisis, the serum was only slightly lytic when tested on the same strain of trypanosomes, but the serum during and after the crisis was very strongly lytic to the original strain. Furthermore, he showed that although the serum taken after or during the crisis was strongly lytic to the original passage strain, it had no deleterious effect on the trypanosomes which reappeared in the guinea pig after the crisis to constitute the relapse. Here is clear experimental proof that the antibody which brought about the crisis remains in the blood (as shown by the activity against the original passage strain) and that the trypanosomes can accumulate again during the relapse due to a change in their biological properties which has made them no longer susceptible to the antibody. Massaglia then not only correlated the production of an antibody with the crisis but he explained the relapse in the uninfluenced course of the infection as being due to the acclimatization of the parasites to the antibody.

Levaditi and Mutermilch (1909), working with *T. brucei* and *T. evansi* in the guinea pig and using much more careful technique, confirmed Massaglia's general conclusions. They showed, furthermore, that when the trypanolysin acted on trypanosomes *in vitro* there was a co-action between a thermolabile nonspe-

cific (alexin or complement) and a thermostable specific (sensitizer or amboceptor) property. They found, also, that between their two species the lysins were specific. They also state that the original passage strain can be made resistant to the lytic antibody by a few minutes contact with the immune serum *in vitro* (as Ehrlich, Roehl and Gulbransen, 1909, had previously done in their studies). This *in vitro* formation of resistant or relapse strains was very carefully studied by Levaditi and McIntosh (1910).

Leger and Ringenbach (1911*a* and *b*) studied the effects of various sera which were lytic to the homologous trypanosome upon heterologous trypanosome species. Although they found them to be in general specific they found the usual group relations manifested in such immunological phenomena.

Ritz (1916) has applied the method of Ehrlich and his co-workers to the differentiation of relapse strains in the uninfluenced infection with *T. brucei* in the rabbit. He worked with a single-cell strain and obtained much the same results as he had previously obtained with mice in which the crises were artificially induced by partial cure with drugs.

Very little is known of the mode of formation of these antibody resistant races of the relapse. The explanation advanced by Ehrlich is an integral part of his general side-chain theory of immunity. He postulated that the protoplasm of the cell was composed stereochemically of a central molecular complex (Leitungskern) with which the basic activities of life were associated and a number of subsidiary molecular groups or side-chains (Seitenketten) with which the purely vegetative functions are associated. Of the side-chains those which could combine with chemical bodies were designated receptors or chemo-

receptors whereas those which combined more or less exclusively with food stuffs were differentiated as nutriceptors. His conception of the formation of a new race of trypanosomes resistant to antibodies is essentially that the nutriceptors of the original strain combine with the trypanocidal antibodies of the host and atrophy, whereupon new receptors are developed by the trypanosomes which will not combine with the antibodies in question, and hence, bring about a relapse. Ehrlich's explanation of the formation of *chemo-resistant* races of trypanosomes is different from this and depends, not on the atrophy of the nutriceptors, but on the modification of the corresponding receptors. In spite of the brilliancy of his experimental work, Ehrlich's hypothesis of "receptor atrophy," though intriguingly simple, is nothing more than the re-statement of the experimental findings in figurative terms.

In the work of Levaditi and McIntosh (1910), when the immune serum from guinea pigs was added to a suspension of the passage trypanosomes, most of the parasites were killed and only a very few remained to be injected into mice to give rise to the resistant strain. This led Levaditi and McIntosh to postulate a process of true selection as the basis for the formation of antibody resistant strains. In the process the susceptible ones perished and the resistant ones repopulated the blood stream.

Rosenthal (1913) gives an hypothesis which really differs from either of the former in that he maintains that the trypanocidal substance in the serum is different from that which causes the trypanosomes to become resistant to the trypanocidal activity. The latter he terms the "relapse substances." This author tested the characteristics of his strains as follows: Mice were infected

with *T. brucei*, cured with tartar emetic or arsacetin, and bled to give the immune serum possessing trypanocidal properties. To test the properties of the trypanosomes in a given mouse it was treated as above with tartar emetic or arsacetin and at the end of several days re-inoculated with the original strain. If it proved to be immune to the second injection, the trypanosomes of the original infection were said to have the properties of the original strain, if it proved not immune, the trypanosomes of its first infection were said to have the properties of the relapse strain. The author based his conclusions on three sets of experimental findings: (1) the trypanocidal property of mouse-immune serum does not vary proportionately to its power to produce relapse strains; (2) the property of producing relapse strains is thermolabile in that it is destroyed when the serum is heated at 60°C. for 15 minutes whereas the trypanocidal property is not altered by this treatment; and (3) the property of forming relapse strains is recovered with the albumen fraction of the serum whereas the trypanocidal property is recovered with both the albumen and the globulin fractions. If these findings are verified, particularly in the case of the trypanolysins arising in the uninfluenced infections in guinea pigs, etc., they will have a marked effect on our knowledge of the formation of these resistant strains.

Any acceptable explanation of the acquisition of a resistance to antibodies will have to take into consideration the fact that the phenomenon is very wide spread among both free-living and parasitic protozoa. The literature is too extensive to give more than a few of the more important developments. Among the trypanosomes, the same phenomenon occurs in regard to other immune properties developed in infected animals, such

as the "protective property" of immune sera. (See especially Mesnil and Brimont, 1909.) It occurs in treatment by drugs. Thus, if an infected animal is imperfectly treated with a trypanocidal drug and a relapse occurs, the trypanosomes are no longer susceptible to a dose of the same drug which would have cured the original infection. (See especially Ehrlich, 1909. For a general review of these "induced variations" in the trypanosomes, see Dobell (1912).) Similar drug-resistant forms can be produced in the free-living species, *Paramecium*. (See Jollos, 1921.)

Certain facts are more or less common to all of these: (1) The acquisition of the resistance occurs within a "pure line" or single-cell strain. Consequently, if Levaditi and McIntosh mean to imply that a true selection of resistant genotypes from a "wild" population of mixed genotypes takes place, their explanation will not hold. (2) Although the resistance is inherited for many generations, it is lost in time. In the case of the parasitic forms, a change of vertebrate host in which it is grown or passage through the invertebrate host causes the strain to revert. In *Paramecium* it is generally quickly lost at conjugation (although it may survive one or two), but not at endomixis (Jollos, 1921). (3) Generally, even in Jollos' work on *Paramecium*, the acquisition of the resistance is associated with the killing off of a large part of the population and is acquired by the survivors very quickly. Thus, it seems to be something of a selection within the "pure line," but one selection is effective, a fact which is in marked contrast to the slow effects of selection of such characters as Jennings and others have studied in the free-living protozoa. (See Jennings, 1920.) The destruction, with its resulting selection, according

to the work of Rosenthal, is not essential, but his results are difficult to apply to the acquisition of resistance to chemicals in the free-living forms. In addition to these general characteristics, it is interesting to note that in the case of the formation of chemical-resistant strains in single-cell strains of *Paramecium*, according to Neuschloz (1919), the acquisition of a resistance to a chemical is associated with the acquisition of the power to destroy the specific chemical or to convert it into a less poisonous compound. Jollos has classified all of these cases of acquired resistance, together with certain other variations which are inherited for a greater or less time, as persistent variations or "Dauermodifikationen" and has thus differentiated them from true mutations.

V. INFECTIONS WITH THE NON-PATHOGENIC TRYPANOSOMES

Although by far the majority of trypanosome species exert no observable ill-effects on their hosts, the only one that has been carefully studied is *T. lewisi*, the non-pathogenic trypanosome of rats. The enumerative studies of Steffen (1921) showed that the number curve in this infection is generally as follows: After an incubation period, the parasites increase in the blood, sometimes attaining over several hundred thousand per cubic millimeter of blood, but if the rat does not die, there is a crisis in the early part of the infection when most of the parasites are destroyed; those that remain continue to live in the blood for some time (varying from several weeks to several months) until a second crisis occurs when all of them are destroyed. Rabinowitsch and Kempner (1899) showed that after the parasites disappear the rat is immune to a second infection. These results have

been fully confirmed by Taliaferro, W. H. and L. G. (1922), Taliaferro (1924) and Coventry (1925). (See fig. 5.)

Many years before exact enumerative studies were made on infections with *T. lewisi*, it was found from microscopical studies of slides made during the course of infections in the rat that during the first part of the infection, when the organisms are increasing in the blood, they are actively reproducing by fission but that during the latter part of the infection they simply exist in the blood as

The progressive daily changes in the reproductive activity of the parasites throughout the entire infection with *T. lewisi* were clearly demonstrated by applying the coefficient of variation method, outlined previously. Thus, the daily rate of reproduction of the parasites was represented mathematically by drawing and measuring 100 parasites from each daily blood smear and calculating the coefficient of variation from these measurements. Coefficient of variation as used here means coefficient of variation for

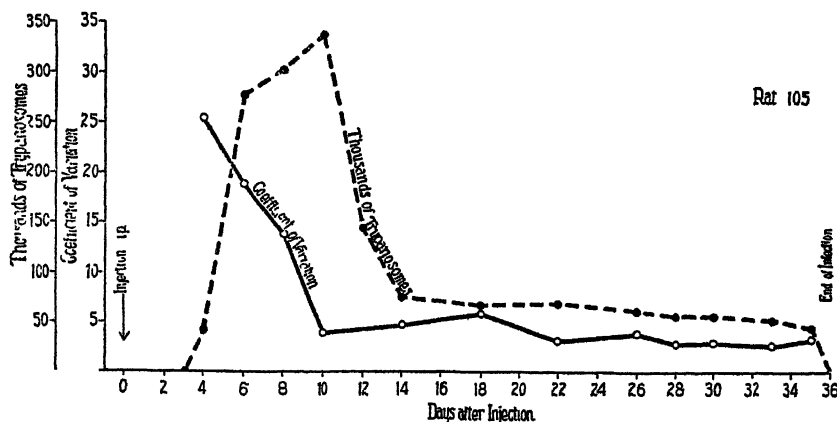


FIG. 5. GRAPH SHOWING THE COEFFICIENT OF VARIATION FOR TOTAL LENGTH (COMPARATIVE MEASURE OF THE RATE OF REPRODUCTION) AND THE NUMBER OF TRYPANOSOMES PER CUBIC MILLIMETER OF BLOOD, THROUGHOUT THE COURSE OF AN INFECTION WITH *T. LEWISI* IN A RAT

This infection illustrates the condition in which there are both an inhibition of reproduction of the parasites, as shown by the drop in the coefficient of variation to about 3 per cent by the tenth day, and a marked parasitocidal action, as shown by the number crisis about the twelfth day and at the end of the infection. (After W. H. Taliaferro.)

non-reproducing adults. This fact was clearly brought out by Rabinowitsch and Kempner (1899) and Wasielewski and Senn (1900). Laveran and Mesnil (1901) confirmed and greatly extended the observations of these earlier workers. Furthermore, the general cessation of reproduction was common knowledge to the protozoologists in succeeding years.

The retardation and final inhibition of reproduction was more accurately studied by the present author with the assistance of L. G. Taliaferro (1922).

total length. Parenthetically, it may be recalled that the higher the rate of reproduction the higher the coefficient of variation will be. Thus, when the organisms first appear in the blood, microscopical examination reveals that they are reproducing at a very rapid rate and calculation for the coefficient of variation likewise gives the very high value of 25 to 30 per cent. The rate of reproduction on succeeding days, however, as expressed by the coefficient of variation, rapidly decreases (25.3, 18.8, 13.8, 3.9 per cent

the fourth, sixth, eighth and tenth days of the blood infection, respectively) until about the tenth day of the infection when no reproduction is found to be taking place at all, at which time the coefficient of variation is around 3 per cent. Reproduction is never resumed thereafter; that

(1) the retardation and final inhibition of reproduction by about the tenth day, (2) the sudden destruction of the majority of the parasites between the eighth and twelfth days, and (3) the eventual total destruction of the parasites which terminates the infection and may take place

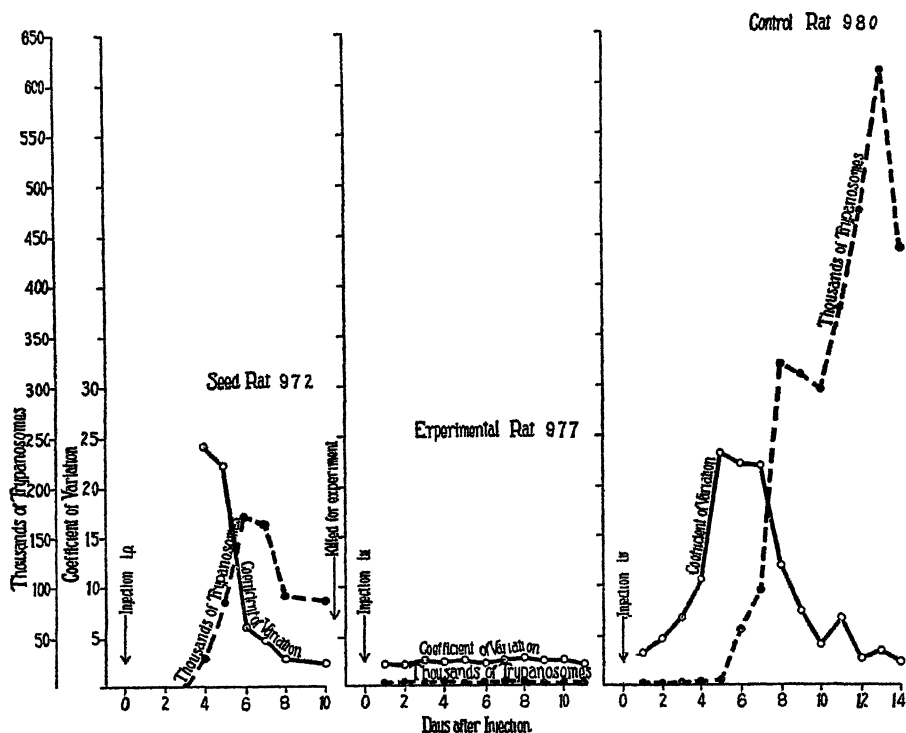


FIG. 6. GRAPHS DEMONSTRATING THE PASSIVE IMMUNIZATION OF AN UNINFECTED RAT WITH THE REPRODUCTION-INHIBITING REACTION PRODUCT WHICH HAS BEEN FORMED IN AN INFECTED RAT

Note that after reproduction had been inhibited in Seed Rat 972, one half of its adult trypanosomes, plus a suitable amount of its serum, was injected into Experimental Rat 977, while the other half of its trypanosomes, plus an equal amount of serum from a normal rat, was injected into Control Rat 980. Subsequently, in Experimental Rat 977 the normal cycle of reproduction was altered—there was a complete inhibition of reproduction as evidenced by the coefficient of variation; whereas in Control Rat 980, the normal cycle of reproduction took place. (The peak in the number curve of Control Rat 980 is so much higher than that of Seed Rat 972 because it received an enormously large number of parasites initially.) (After W. H. Taliaferro.)

is to say, the coefficient of variation remains in the vicinity of 3 per cent throughout the remainder of the infection, which may, in some cases, as previously stated, extend over a period of several months.

From this work it may be said that there are three manifestations of resistance:

from a few days to several months after the first crisis.

The immunological basis of the first effect of resistance has been studied by the present author (1924). His work indicates that the inhibition of reproduction is due to the acquisition of a property of

the serum in the infected rat which has the peculiar property of inhibiting reproduction but which does not kill the trypanosomes. The method of demonstrating the presence of this property or reaction product is shown in figure 6 which is an example from numerous experiments carried out by the author (1924) and Coventry (1925). First, an infection in a rat (seed rat 972) was allowed to progress until the tenth day when the parasites were no longer reproducing and the coefficient of variation was in consequence 3 per cent. The rat was then killed and bled, and its serum collected. The serum (which contains the reaction product or immune body) was separated from the adult trypanosomes present by centrifugation. This serum in a dose of 2 cc. per 100 grams of rat together with half of the adult trypanosomes was injected intravenously into experimental rat 977 while a similar dose of *normal* serum together with the other half of the adult trypanosomes was injected intravenously into control rat 980. Daily examinations and calculations for the coefficient of variation for total length for these two rats showed that the trypanosomes in experimental rat 977 lived in the blood for eleven days (infection died out at this time) without showing any reproduction (the coefficient of variation never exceeded 3 per cent, and furthermore, the organisms never increased in the blood and no dividing parasites could be found); whereas in control rat 980 reproduction began on the second day and followed the course of a normal infection (the coefficient reached the high peak of 25 per cent between the fourth and sixth days, and as was to be expected, the organisms showed a marked increase in numbers in the blood and many dividing parasites were found). In these experiments it is to be noted that not only

did the immune serum, viz., the serum taken from the seed rat on the tenth day, prevent "adult" trypanosomes from reproducing in a new rat, but that normal rat serum did not prevent similar adult parasites from reproducing in a similar new rat. This is a clear-cut case of the passive transfer of the immunity from an infected to an uninfected rat.

The changes in titer of this reaction product through the course of an ordinary infection has been studied in detail by Coventry (1925). She was unable to demonstrate its presence in serum prior to the fifth day of the infection although it is probably present since by the fifth day the rate of reproduction has already begun to decrease. She found a sudden and very great increase in its titer between the fifth and sixth days of the infection with a subsequent gradual increase until the thirty-fifth day after which there was a gradual decrease.

As the formation of this reaction product, which inhibits the reproduction of the parasites without affecting their vitality, emphasizes a new effect of resistance, the present author has attempted to compare it with other known immune bodies (unpublished work and Taliaferro, 1925). Like most reaction products or antibodies, this one is non-ether soluble and is precipitated with the globulin fraction of the immune serum. Strange to say, it comes down equally with the eu- and pseudoglobulin. It differs from others, however, in its lack of *in vitro* affinity for its supposed antigen. Thus, when serum containing it is left in contact for 12 hours with large numbers of dividing *T. lewisi* and the parasites subsequently removed, the serum does not lose any of its titer.

As far as the author is aware there has been neither any experimental work nor any explanation advanced to account for

the second manifestation of resistance, i.e., the first number crisis which occurs between the eighth and twelfth day of the infection.

Some work, however, on the immunological basis for the immunity of recovered rats to a second infection with *T. lewisi*, has been done and probably explains the third manifestation of resistance, i.e., the crisis which terminates the infection. Laveran and Mesnil (1901) came to the conclusion that this immunity as well as the final disappearance of the parasites is due to the phagocytosis of the living trypanosomes. MacNeal (1904), on the other hand, has obtained experimental evidence that the final disappearance of the trypanosomes is due to a trypanolytic process, just as has already been described for the crises in the pathogenic forms. Manteufel (1909) also holds that phagocytosis is only a secondary function and that the immunity rests upon the trypanocidal or trypanolytic property of the serum. The present author (1924) has confirmed MacNeal's work that a lysin is formed at the termination of the infection. His work indicates, however, that this lysin which terminates the infection disappears from the blood and is not the basis of future immunity, but that this is bound up with the reproduction-inhibiting reaction product described above. Let us consider how this might be. A rat recovered from an infection of *T. lewisi* possesses, let us say, in its bloodstream the reproduction-inhibiting reaction product but no trypanolysin. Under ordinary conditions it receives comparatively few forms from either injection or from infected fleas. These find their way, eventually, into the blood and exist there, at least for a time, but being unable to reproduce, can not set up infection. During this time even though examinations of the blood are made no trypanosomes are

found because they have been dispersed throughout the rat. The reproduction-inhibiting reaction product, therefore, prevents the occurrence of a normal infection although it allows a few stray forms to live on in the blood.

VI. COMPARISON OF THE LETHAL AND NON-LETHAL TRYPANOSOMES

A consideration of all of the known trypanosome species brings out the fact that most of them are, as far as can be seen, non-pathogenic parasites (commensals) just as *T. lewisi* is in rats. There is a growing mass of evidence that even many of the well-known pathogenic forms, which produce such fatal diseases in man and domesticated animals, live as non-pathogenic forms in their natural vertebrate hosts. Thus, *T. gambiense* may be a harmless commensal of the antelope and other wild game of Africa. This at once leads to the suggestion that whether or not a given species is pathogenic depends upon the reactions of the host. A comparison of the resistance which a host acquires against the pathogenic forms and the resistance of the rat against the non-pathogenic *T. lewisi* is very interesting in this connection. It has been seen that in the pathogenic trypanosomiasis, the host either acquires no resistance (mouse) or periodically forms a trypanolysin which produces a number crisis (guinea pig, dog, etc.). In the second case, the resistance is never permanently effective because the parasites are never all killed and those which remain, after becoming resistant to the antibody, can continue to reproduce at a uniform rate. In the non-pathogenic *T. lewisi*, however, the host first produces an antibody which completely inhibits reproduction (cell-division) in the parasites. Thereafter, each number crisis is so much gained by the host be-

cause the parasites cannot re-populate the blood stream even if they should become resistant to the trypanocidal mechanism. It is possible then that the formation of a reproduction-inhibiting reaction product, in conjunction with trypanocidal antibodies, would convert an otherwise lethal parasite into a non-lethal one. Van Saceghem (1923) suggests that the presence of such a reproduction-inhibiting property causes the pathogenic trypanosomes to become harmless commensals in wild animals. Brown (1914^a and *b*) has studied a strain of *T. lewisi*, which was pathogenic to rats. In considering his second paper, the chief anomalies of his pathogenic strain can be explained on the assumption that it continued to reproduce much longer than normal strains. This indicates that in a rat no longer capable of forming the reproduction-inhibiting antibody, the parasite becomes pathogenic. Similarly, the author has observed apparent lethal infections with *T. lewisi* in which the reproduction of the parasites was never completely inhibited.

Another example of the so-called pathogenic trypanosomes becoming non-lethal to their hosts is seen in the Bovidae. Most of our knowledge of this type of infection, which has been fully described by Laveran (1911) and Mesnil and Leger (1912), has been derived from work on goats and sheep where the infection is generally of such a low grade that the parasites can not be found by microscopical examination but their presence can be demonstrated by subinoculations into mice. Such an infection persists for from one to several months whereupon the host recovers and is more or less refractory to a second infection with the same species of trypanosome. It is, of course, impossible to analyse the effects of resistance in this type of infection as

we have done in the preceding infections because the trypanosomes can not be found microscopically in the blood. Similarly, there is little indication of what the immunological basis for this type of infection may be.

One outstanding feature of the serum of animals that show a chronic (*viz.*, sheep) or even sub-acute (*viz.*, the rabbit) infection is that it is *protective*. If serum from such an infected animal be injected simultaneously with trypanosomes from the passage strain, it will either delay or completely inhibit the infection. Such serum is not curative, *i.e.*, it does not prolong the life of mice if injected after the infection has progressed for even a day or so.

This immune property will only be mentioned since, so far, there is no direct evidence that it is connected with, or is the basis for, the chronic or low grade type of infection. The protective property of immune serum was probably first observed by Rouget (1896) who found that the serum of rabbits and dogs which were infected with *T. equiperdum* and had become cachectic exerted a protective action on mice infected with the same trypanosome, as measured by their survival time. By far the most careful work on it was done by Mesnil and Brimont (1909) who worked with *T. evansi*, *T. brucei* and *T. togolense* (= nagana of Togoland).

In the consideration of the pathogenic trypanosomes in various laboratory animals, it has been stated repeatedly that reproduction occurs uniformly throughout the infection. Some of the work of Robertson (1912) on *T. gambiense* in the monkey indicates that an endogenous cycle of reproduction occurs in which phases of active reproduction alternate with phases of lessened reproduction. She measured the rate of reproduction by ascertaining the percentage of dividing

forms on successive days—a method which is undoubtedly valid but which possesses a drawback in that the comparative scarcity of dividing forms makes it difficult to obtain statistically valid samples. With her data, however, which contains the length of trypanosomes from day to day, the present author has applied his coefficient of variation method and has found that Robertson's conclusions are sound, but that even at the periods of least reproduction, reproduction is nevertheless occurring at a comparatively high rate.

VII. MALARIAL INFECTIONS

Among the malarial parasites, the most complete knowledge of the course of the infection has been obtained from a study of *Plasmodium relictum*, the parasite of sparrows and probably of other birds. This is due to the fact that this organism is well-adapted to laboratory work not only because it is easily grown in the domestic canary but can be transmitted from one bird to another by injections of infected blood. Our knowledge of the

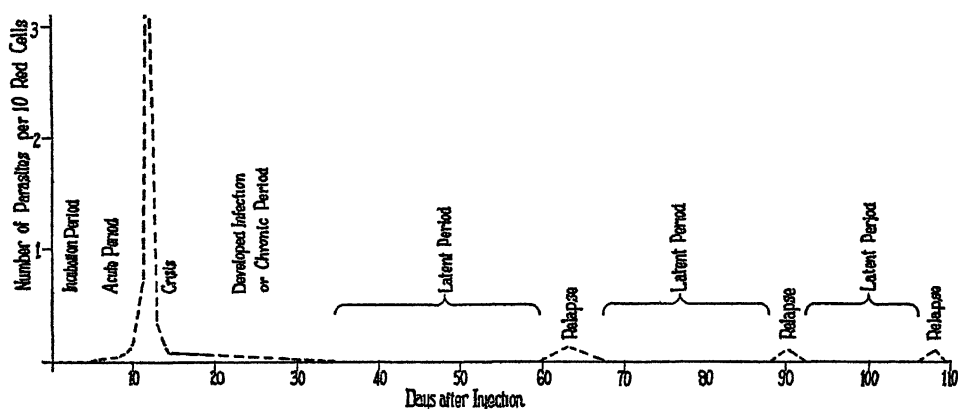


FIG. 7. GRAPH ILLUSTRATING THE COURSE OF AN INFECTION OF *PLASMODIUM RELICTUM* IN THE CANARY

Furthermore, there is some evidence that the original strains of parasites in Africa show these alternate phases of reproductive activity, but that by continuous subinoculation in the laboratory, the rate becomes constant. Consequently, although Robertson's results are of a great theoretical interest, they do not invalidate the general deductions made in this and other sections on the pathogenic trypanosomes, since reproduction was never completely and permanently inhibited, as in the case with *T. lewisi* in the rat.

progressive changes in the number of parasites in the blood has accumulated from the work of many investigators. Exact enumerative studies have been made by the Sergents (see especially 1918), Ben Harel (1923), Taliaferro, L. G. (1925) and Boyd (1925).

In general the course of the infection may be divided into the following periods, as is shown in figure 7: (1) After the introduction of the parasites (whether by the bite of a mosquito or injection) there is an incubation period during which no

parasites can be found in the blood and the length of which is, according to Boyd, largely correlated with the number of parasites received. (2) The acute stage is initiated when they appear in the blood and extends over a period of 3 or 4 days (sometimes more) during which the parasites are rapidly increasing in number. According to L. G. Taliaferro (1925), the rate of this increase is uniform and follows the formula for a geometrical progression series. Even during this acute period when the number of parasites

the developed infection. During this period, comparatively few parasites are found in the blood although they may fluctuate in numbers to a certain extent. (5) In time all of the parasites apparently disappear from the blood and give rise to what is termed the latent period. Although they cannot be found, a few parasites must be present since Whitmore (1918) has shown that blood taken at this time is infective to other birds, and Mazza (1924) has found a bird infective 4 years and 2 months after infection. (6)

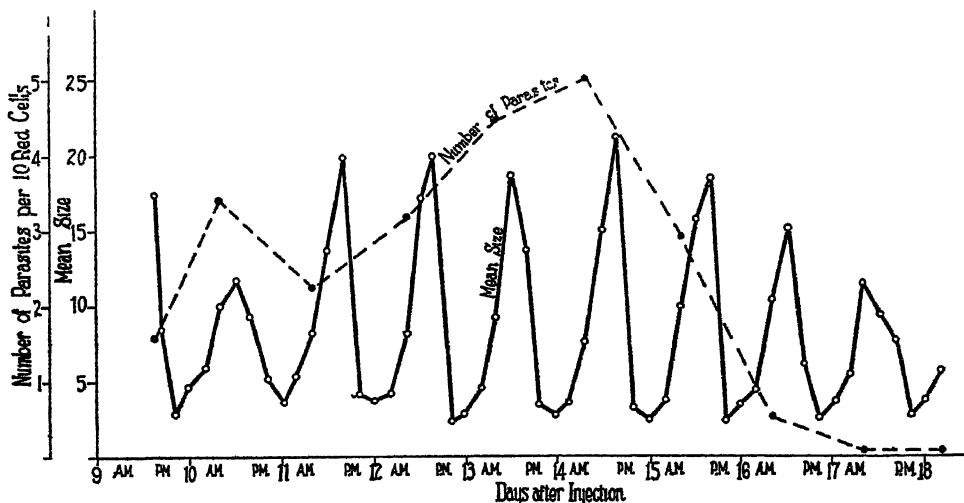


FIG. 8. ACUTE INFECTION AND CRISIS IN AN INFECTION WITH *P. RELICTUM* IN A CANARY SHOWING THE MEAN SIZE OF THE ASEQUAL FORMS AT 4-HOUR INTERVALS AND THE NUMBER OF PARASITES PER 10 RED BLOOD CELLS

The distance between peaks of the mean is a measure of the rate of reproduction which is independent of the number of parasites destroyed. (From data by L. G. Taliaferro.)

are increasing most of the young merozoites produced at each sporulation die (L. G. Taliaferro, 1925). Hartman (1926) has made a very careful study of the mortality at this time. (3) If the bird does not die, the acute period is terminated by a crisis which sweeps the majority of the parasites from the blood. Sometimes there may be several acute rises in the number of parasites, each followed by a crisis. (4) Following the crisis, a low grade infection ensues which is variously termed the chronic stage or

At any time during the latent period the injection of adrenalin or any condition which lowers the bodily resistance of the host, such as exposure, etc., may cause the parasites to reappear in the blood. Such a reappearance is called a relapse.

The number crises which terminate the acute, chronic and relapse periods leave little doubt that some type of resistance is acquired which destroys large numbers of the parasites after they are formed. Unlike *T. lewisi*, however, this is not associated with any retardation of the

rate of reproduction of the parasites according to an extensive study made by L. G. Taliaferro (1925). By using, as a measurement of the rate of reproduction, the length of time necessary for each asexual generation, which has already been explained, she found that no matter when the organisms are studied, whether in the acute, chronic or relapse periods, the length of the asexual cycle is the same (24 hours in one strain). This fact, in conjunction with the fact that the average number of merozoites produced by each mature segmenter does not vary, furnishes evidence for the conclusion given above that there is no noticeable effect on the rate of reproduction *per se*. One interesting fact disclosed in this work is that although the parasites can not be studied in the latent period she found that each stage in the cycle took place at just the same time in the relapse as it did in the acute and chronic periods indicating that the asexual cycle had continued undisturbed throughout the latent period. She gives the following as the probable effects of resistance.

In conclusion, it seems that the probable picture of an infection with bird malaria is somewhat as follows: After the incubation period the asexual stages of the parasites are to be found in the peripheral blood in varying numbers during the entire course of the infection and undergo their cycle of development and reproduction at the same rate throughout. From the very beginning, only a number of the merozoites are viable, this probably represents a natural resistance of the host. During the first part of the infection relatively few parasites are killed, so that they accumulate in the blood and give rise to the acute stage of the infection. Sooner or later, however, as the acquired resistance is built up, a large proportion of the parasites are killed. There may then be a temporary relapse, but eventually the destruction of the parasites equalizes or exceeds the number produced by reproduction, and the chronic period or low grade of blood infection ensues. In time, the destruction becomes so great that no parasites can be found in the blood (latent period), but their presence can be demonstrated by Whitmore's

technique. This continues until some condition, such as the injection of adrenalin, temporarily stops the destruction and the parasites accumulate again, causing a relapse.

It is difficult to study uninfluenced infections of malaria in man because most of them are treated with quinine. Ross and Thomson (1910b) have, however, made a very precise enumerative study of the human infection. From the general experience of most workers it seems probable that the course of the infection of both *P. vivax*, the benign tertian parasite of man, and *P. malariae*, the parasite of quartan fever, is very similar to that of bird malaria. *P. falciparum*, the parasite of malignant tertian fever of man as well as certain avian malarial parasites, on the other hand, offer difficulties in analysing the effect of resistance because as a rule only sexual stages occur in the peripheral blood, the asexual cycle taking place in the capillaries of the internal organs where it is inaccessible for study.

There is no conclusive evidence as to the immunological basis for the destruction of the malarial parasites which occurs to such a great degree at the crises and to a lesser extent throughout the rest of the infection. At these times, Ben Harel (1923) has noted a marked increase in the number of large mononuclear phagocytes in which, furthermore, she has observed some evidences of parasitic phagocytosis. Consequently, she believes that the increase in mononuclears is associated with the decrease of the parasites. It is also a well-known fact that after the crisis, a marked splenomegaly occurs, and that large numbers of parasites in various stages of disintegration can be found in the spleen during this time. No evidence is at present available, however, to show whether these wandering mononuclears and fixed-tissue phagocytes of the spleen and other organs are the pri-

mary cause of the destruction or are simply clearing up debris in the form of parasites already killed by some other agency.

VIII. CONCLUSIONS

As this review is itself essentially a summary, the author will list here only a few of the more salient facts which have been brought out by the present discussion. The authorities for these statements may be found under the sections listed at the end of each statement.

1. After blood parasites, such as are considered in this paper, have successfully invaded their hosts, if there is no resistance operative, they will increase in the blood uniformly according to a geometrical progression series (Section II).

2. The acquired resistance of the host can modify such a uniform increase in one or both of two different ways: (1) by parasiticial effects, i.e., by killing the parasites after they are formed; or (2) by inhibiting their rate of reproduction (Section II).

3. The sum total of the effects of the host's resistance can be evaluated by studying the daily changes in the number of parasites throughout the course of the infection. By using indirect measures of the rate of reproduction of the parasites (coefficient of variation for total length in the trypanosomes or changes in mean size in the malarial organisms), in conjunction with the number curve, the two effects of the host's resistance can be differentiated (Section II).

4. In the pathogenic trypanosomes in the mouse, the host acquires no appre-

ciable resistance, either affecting the rate of reproduction or exerting parasiticial effects on the trypanosomes (Section III).

5. If the same pathogenic trypanosomes are grown in such hosts as the guinea pig, there is no effect on the rate of reproduction, but there are parasiticial effects causing periodic number crises. These crises result from the production of trypanolysins. These lysins remain in the blood, and, if the host does not die, the parasites become changed biologically so that they are resistant to the antibody, and hence, are able to re-populate the blood stream (Section IV).

6. In infections with *Trypanosoma lewisi* in the rat, resistance manifests itself both in parasiticial effects (number crises) and in the inhibition of reproduction of the parasites. The parasiticial effects may be due (at least at the termination of the infection) to trypanolysins. The inhibition of reproduction is the result of the acquisition of a property by the immune serum which prevents cell division of the parasites, but which does not kill them (Section V).

7. The relation between the pathogenic and non-pathogenic trypanosome infections is discussed in detail (Section VI).

8. In the malaria parasite of birds (*Plasmodium relictum*), a marked parasiticial effect of resistance is manifested both at definite number crises and throughout the latter part of the infection. This is, however, not associated with any inhibition of the reproduction of the parasites. The immunological basis for the parasiticial effects are not definitely known (Section VII)

LIST OF LITERATURE

- BEN HAREL, S. 1923. Studies of bird malaria in relation to the mechanism of relapse. *Amer. Jour. Hyg.*, 3: 652-685.
- BOYD, G. H. 1925. The influence of certain experimental factors upon the course of infections with *Plasmodium praecox*. *Amer. Jour. Hyg.*, 5: 818-838.
- BROWN, W. H. 1914a. A note on the pathogenicity of *Trypanosoma lewisi*. *Jour. Exp. Med.*, 19: 406-410.
- BROWN, W. H. 1914b. Morphological and developmental anomalies of a pathogenic strain of *Trypanosoma lewisi* and their relation to its virulence. *Jour. Exp. Med.*, 19: 562-569.
- COVENTRY, F. A. 1925. The reaction product which inhibits reproduction of the trypanosomes in infections with *Trypanosoma lewisi*, with reference to its changes in titer throughout the course of the infection. *Amer. Jour. Hyg.*, 5: 127-144.
- DOBELL, C. 1912. Some recent work on mutation in microorganisms. *Jour. Genetics*, 2: 201-220.
- EHRLICH, P. 1909. Ueber Partialfunktionen der Zelle. *Münch. med. Wchnschr.*, 56: 217-222.
- EHRLICH, P., ROEHL, W. AND GULBRANSEN, R. 1909. Ueber serumfeste Trypanosomenstämme. *Zeit. Immunitätsf.*, 3: 296-299.
- EHRLICH, P. AND SEIGA, K. 1904. Farbentherapeutische Versuche bei Trypanosomenkrankung. *Berl. klin. Wchnschr.*, 41: 329-332 and 362-365.
- FANTHAM, H. B. AND THOMSON, J. G. 1911. Enumerative studies on *Trypanosoma gambiense* and *Trypanosoma rhodesiense* in rats, guinea-pigs and rabbits; periodic variations disclosed. *Proc. Roy. Soc.*, B. 83: 206-211.
- FRANK, E. 1905. Therapeutische Versuche bei Trypanosomenkrankung. *Inaug. Diss. Giessen*.
- HALBERSTADTER, L. 1905. Untersuchungen bei experimentellen Trypanosomenkrankungen. *Centralb. Bakt. Orig.*, 38: 525-532.
- HARTMAN, E. 1926. Parasite mortality in the asexual cycle of bird malaria. *Jour. Parasit.*, 12: (In: *Proc. Amer. Soc. Parasitologists.*)
- HENNER, R. W. AND TALIAFERRO, W. H. 1924. *Human Protozoology*. New York. 597 pp.
- JENNINGS, H. S. 1920. *Life and Death, Heredity and Evolution in Unicellular Organisms*. Boston. 229 pp.
- JOLLOS, V. 1921. Experimentelle Protistenstudien. 1. Untersuchungen über Variabilität und Vererbung bei Infusorien. *Arch. Protistenk.*, 43: 1-222.
- LAVERAN, A. AND MESNIL, F. 1901. Recherches morphologiques et expérimentales sur le trypanosome des rats (*Tr. Lewis. Kent*). *Ann. Inst. Pasteur*, 15: 673-714.
- LAVERAN, A. 1911. Resistance des chèvres et des moutons aux trypanosomiasés; longue durée de l'immunité acquise à la suite de ces maladies. *C. R. Acad. Sci.*, 152: 63-66.
- LEGER, A. AND RINGENBACH, J. 1911. Sur la spécificité de la propriété trypanolytique des sérums des animaux trypanosomiés. *C. R. Soc. Biol.*, 70: 343-345.
- LEGER, A. AND RINGENBACH, J. 1912. Sur la spécificité de la propriété trypanolytique des sérums des animaux trypanosomiés (deuxième note). *C. R. Soc. Biol.*, 72: 267-269.
- LEVADITI, C. AND MCINTOSH. 1910. Mécanisme de la création de races de trypanosomes résistantes aux anticorps. *Bull. Soc. Path. Exot.*, 3: 368-376.
- LEVADITI, C. AND MUTERMILCH, S. 1909. Recherches sur la méthode de Bordet et Gengou appliquée à l'étude des trypanosomiasés. *Zeit. Immunitätsf., Orig.*, 2: 702-722.
- LINGARD, A. 1904. The *Trypanosoma* of dourine and its life history. *Centralb. Bakt., Orig.*, 37: 537-547.
- MACNEAL, W. J. 1904. The life history of *Trypanosoma lewisi* and *Trypanosoma brucei*. *Jour. Inf. Dis.*, 1: 517-543.
- MANTEUFFEL. 1909. Studien über die Trypanosomiasis der Ratten mit Berücksichtigung der Übertragung unter natürlichen Verhältnissen und der Immunität. *Arb. a. d. Kais. Gesundh.*, 33: 46-83.
- MASSAGLIA, M. A. 1907. Des causes des crises trypanolytiques et des rechutes qui les suivent. *C. R. Acad. Sci.*, 145: 687-689.
- MAZZA, S. 1924. On the duration of relative immunity in malaria of birds. *Jour. Trop. Med. and Hyg.*, 27: 98-99.
- MESNIL, F. AND BRIMONT, E. 1909. Sur les propriétés protectrices du sérum des animaux trypanosomiés.—Races résistantes à ces sérums. *Ann. Inst. Pasteur*, 23: 129-154.
- MESNIL, F. AND LEGER, M. 1912. Documents relatifs au Surra des Caprins et à leur immunité. *Bull. Soc. Path. Exot.*, 5: 31-35.
- MUTERMILCH, S. 1911. Sur l'origine des anticorps chez les cobayes Trypanosomiés. *Ann. Inst. Pasteur*, 25: 776-784.
- NEUSCHLOSZ, S. 1919. Untersuchungen über die Gewöhnung an Gifte. I. *Pflügers Arch.*, 176: 223-235. II. *Ibid.*, (1920) 178: 61-68. III. *Ibid.*, (1920) 178: 69-79.

- RABINOWITSCH, L. AND KEMPNER, W. 1899. Beitrag zur Kenntniss der Blutparasiten, speciell der Rattentrypanosomen. Zeit. Hyg. und Infektionsk., 30: 251-294.
- RITZ, H. 1914. Ueber Rezidive bei experimenteller Trypanosomiasis. Deutsch. med. Wchnschr., 40: 1355-1358.
- RITZ, H. 1916. Ueber Rezidive bei experimenteller Trypanosomiasis. II. Mitteilung. Arch. Schiffs- und Trop.-Hyg., 20: 397-420.
- ROBERTSON, M. 1912. Notes on the polymorphism of *Trypanosoma gambiense* in the blood and its relation to the exogenous cycle in *Glossina palpalis*. Proc. Roy. Soc. Lon. B 85: 527-539. Reports Sleeping Sickness Com. Roy. Soc., No. 13: 94-110.
- RODET, A. AND VALLET, G. 1906. Contribution à l'étude des trypanosomiasis. Recherches expérimentales sur le *Trypanosoma brucei*. Arch. Méd. Expér. et Anat. Path., 18: 450-494.
- ROSENTHAL, F. 1913. Untersuchungen über die Genese des Rezidivs bei der experimentellen Trypanosomeninfektion. Zeit. Hyg. und Infektionsk., 74: 489-538.
- ROSS, R. AND THOMSON, D. 1910a. A case of sleeping sickness studied by precise enumerative methods; regular periodical increase of the parasites disclosed. Proc. Roy. Soc., Lon., B 82: 411-415.
- ROSS, R. AND THOMSON, D. 1910b. Some enumerative studies on malarial fever. Proc. Roy. Soc., Lon., B 83: 159-173.
- ROUGET, J. 1896. Contribution à l'étude du trypanosome des mammifères. Ann. Inst. Pasteur, 10: 716-728.
- VAN SACCHS, R. 1913. Le pouvoir empêchant dans les trypanosomiasis. Bull. Soc. Path. Exot., 16: 733-735.
- SERGEANT, E. AND E. 1918. Sur le paludisme des oiseaux de au *Plasmodium relictum* (vel *Protozoma*). Ann. Inst. Pasteur. 32: 382-388.
- SCHILLING. 1902. Bericht über die Surra-Krankheit der Pferde und Rinder im Schutzgebiete Togo. Centralb. Bakt., Orig., 31: 452-459.
- STEFFAN, P. 1921. Beobachtungen über den Verlauf der künstlichen Infektion der Ratte mit *Trypanosoma lewisi*. Arch. Schiffs- und Trop.-Hyg., 25: 241-247.
- TALIAFERRO, L. G. 1925. Infection and resistance in bird malaria, with special reference to periodicity and rate of reproduction of the parasite. Amer. Jour. Hyg., 5: 742-789.
- TALIAFERRO, W. H. 1922. A study of size and variability, throughout the course of "pure line" infections, with *Trypanosoma lewisi*. Jour. Exp. Zool., 37: 127-167.
- TALIAFERRO, W. H. 1924. A reaction product in infections with *Trypanosoma lewisi* which inhibits the reproduction of the trypanosomes. Jour. Exp. Med., 39: 171-190.
- TALIAFERRO, W. H. 1925. Properties of the reproduction-inhibiting reaction product in infections with *Trypanosoma lewisi*. Anat. Record, 31: 314.
- TALIAFERRO, W. H. AND L. G. 1922. The resistance of different hosts to experimental trypanosome infections, with especial reference to a new method of measuring this resistance. Amer. Jour. Hyg., 2: 264-319.
- THOMSON, J. G. 1912. Enumerative studies on *T. brucei* in rats and guinea-pigs and a comparison with *T. rhodesiense* and *T. gambiense*. Ann. Trop. Med. and Parasit., 5: 531-536.
- V. WASILEWSKI AND SENN, G. 1900. Beiträge zur Kenntniss der Flagellaten des Rattenblutes. Zeit. Hyg. u. Infektionsk., 33: 444-471.
- WELLS, H. G. 1925. The Chemical Aspects of Immunity. New York. 254 pp.
- WHITMORE, E. R. 1918. Observations on bird malaria and the pathogenesis of relapse in human malaria. Johns Hopkins Hosp. Bull., 29: 62-67.





FREEZING AND SURVIVAL OF INSECTS AT LOW TEMPERATURES

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EXTREMES of temperature are important factors in the ecology of all animals. Low temperatures affect the geographical distribution of insects, their cold resistance, rate of metabolism, behavior, and in some cases even their color and structure. This paper is the result of studies of the effect of low temperatures on cold resistance in insects with especial reference to temperatures below the freezing point of water.

Three ecological groups of insects were chosen for study: (1) the oak borers living close to the outer surface of the bark, normally exposed to extremes of low temperature; (2) aquatic insects living in lakes, never exposed to temperatures lower than 0°C.; (3) insects infesting stored products.

The necessity for the endurance of low temperature is a fundamental one which must be met by all organisms living in Northern climates. The literature on the biological effects of low temperatures is enormous. Literature relating to both plants and animals is cited in this paper for the reason that plant physiology has been advanced to a farther stage than insect physiology and offers many suggestions to workers in the animal field.

I. LITERATURE ON THE EFFECTS OF LOW TEMPERATURE ON PLANTS

There is an extensive and scattered literature on the freezing and hardening

in plants and on allied physiological effects of cold. It is interesting to discover that very early in the history of plant physiology, observations took on a quantitative aspect. Workers in this field of plant physiology include some of the foremost plant physiologists, as for example, Sachs and Pfeffer.

In plants, death from freezing has been considered to be due to the following causes: (1) mechanical injury from ice crystal formation, (2) water loss either direct or indirect through permeability changes in the cell membrane, (3) precipitation of proteins or other irreversible chemical effects. The order given in general follows the historic development of the study of cold effects on plants.

Duhamel and Buffon (1732) held that death from freezing was due to the rupture of tissue from ice crystals formed in freezing. Morren (1852) found no histological evidence in favor of this theory. Göppert (1829) found that ice formation took place in both cells and cellular spaces. Sachs (1860) discovered that in the process of freezing water was withdrawn from the cells to freeze for the most part in the intercellular spaces. From another source evidence was obtained against the cell-rupture theory when Nägeli (1860) calculated the expansion of all the water in a cell at freezing and found that the total expansion was insufficient to cause rupture. However, disproving that cell rupture is the cause

of death from low temperatures is not the equivalent of finding the cause of death from low temperatures, nor does the negative result obtained throw much light on the subject of death from this cause.

Water loss both direct and indirect was the next explanation for injury and death at low temperatures. Water loss from frozen tissue on thawing was observed by Göppert (1829). Prilleux (1869) discovered that water was exuded from the cells in the freezing process. Sachs (1860) noted that water exuded from the cells was "reabsorbed" or was lost by evaporation. Injury from freezing was thought to be due essentially to a dehydration. Another effect of low temperature analogous to the effect from freezing was dehydration at low temperatures above the freezing point. Water intake and water transportation at low temperatures is not rapid enough to balance transpiration. The plant exposed to such temperatures may wilt and finally die from the effects of low temperature without ever being frozen. Sachs (1860) points out these two dehydration effects of low temperature.

As an outgrowth of the more simple theory of direct water loss comes the theory of injury from water loss due to alteration of the permeability of the cell membrane at the time of freezing. Loss of water according to this view is not the primary cause of death from freezing, but permeability changes are. Maximow (1912) worked on sections of red cabbage and *Tradescantia*. He came to the conclusion that the part of the plant that was injured by low temperature was the plasma membrane. The immersion of sections of plant tissue in various solutions influenced the freezing point. Substances that enabled the cells to withstand a lower temperature than normally were called "Schützmittel" or protective sub-

stances. The degree of protection afforded by different substances was proportional to the eutectic point when the molecular concentrations were the same. Chandler (1913) came to the conclusion that the cause of death from freezing was due to mechanical injury of the plasma membrane. Death from freezing was limited to one condition, namely, the condition of brown wilted tissue resulting from exposure to freezing temperatures and subsequent thawing. Poor metabolism due to low temperature was not studied in Chandler's paper.

The third theory considers protein precipitation in the frozen cells accountable for death from freezing. The first man to elaborate this theory was Gorke (1906). His evidence was derived from plant cells and from solutions of proteins. The degree of hardness in plants was correlated with the ease or difficulty with which their proteins were precipitated. In non-hardy begonia leaves protein precipitation took place at $-3^{\circ}\text{C}.$, in rye at $-15^{\circ}\text{C}.$, and in pine needles at $-40^{\circ}\text{C}.$ Schaffnit (1910) found that rye protein from plants grown under greenhouse conditions was more easily precipitated than rye protein from plants grown under outdoor conditions. Schaffnit's work will be taken up again when hardness is discussed. Harvey (1918) found that a correlation existed between protein precipitation and hardness. The influence of increased sugar content noted by Lidforss (1907), by Schaffnit (1910), and by later workers may be primarily as a protection to the proteins against precipitation, although such solutes would also lower the freezing point. Harvey (1919) laid emphasis on the relation of epidermal coverings to undercooling. He considered that concentration of cell solutes played a minor rôle in the determination of cold resistance in plants, the

principal effect coming from the precipitation of protein under the changed conditions produced by ice formation.

The development of hardiness in plants and the correlation of physical condition of cell colloids and of osmotic concentration of solutes with hardiness, is at present one of the extensively cultivated fields of plant physiology. By hardiness is meant the resistance of plants to low temperatures. Harvey has defined this term as the ability of a plant to survive ice formation within the tissues. The present writer uses the more general definition given first on account of the fact that the term hardiness has been used in the broader sense in much plant literature, and also for the reason that cold resistance in animals has not been studied sufficiently for us to know definitely the underlying cell changes that are responsible for increased resistance to cold.

Plant hardiness has long been of interest in horticulture and agriculture. Efforts to produce frost hardy plants are some of the new developments arising from the application of plant physiology and genetics. Factors that make for plant hardiness were studied in detail by Gorke (1906). Schaffnit (1910) found that cold hardiness in rye was increased by exposure of rye to low temperatures during growth. Lidforss (1907) noted that the sugar content of pine needles increased with the oncoming of winter. Maximow (1912) found that he could induce hardiness in plant tissues by soaking them in solutions of non-toxic substances. Among the substances used were glycerine, sucrose, mannite, and various nitrate salts. Rosa (1921) comes to the conclusion that any process which will bring about a material decrease in the rate of growth will result in an increase in hardiness. Decreasing the water content, increasing the amount of hydro-

phylic colloids present or increasing the water holding capacity of these colloids will result in an increase of hardiness, according to this investigator. Harvey (1918) studied the development of hardiness in plants and comes to the following conclusion.

The principal effect of the hardening process for cabbages is a change in the constituents of the protoplasm which prevents their precipitation as a result of the physical changes incident upon freezing. The proteins are changed to forms which are less easily precipitated. This is indicated by an increase in the amino-acid content of the cabbage plants on hardening.

. . . . The effects of desiccation, freezing, and plasmolysis are considered to be similar in that all these processes cause changes in the hydrogen-ion and salt concentration.

Studies on the concentration of the sap and its relation to hardiness have been made by Gortner and Harris (1914). Tropical plants have a lower osmotic concentration and a lower pressure than do plants of temperate zones. Newton (1924) worked on the relation of the concentration of cell sap to the winter killing of different varieties of wheat. The ability of the cell colloids to adsorb water was taken as a measure of the cold resistance of winter wheat. The process of hardening in this case is thought to be the process of water adsorption and water retention by the hydrophilic colloids.

The relation of water content to winter hardiness was stressed by Johnson (1919, 1921, and 1923). He used water content as an index to the hardiness of peach buds. Newton (1924) found that water content of winter wheat was a partial index to hardiness.

There is another aspect to the subject of freezing that was brought out by Müller-Thurgau (1880). He distinguished between freezing and death from freezing. He also contributed to the theory of

freezing and made valuable observations on low temperatures of trees in winter.

Göppert (1839) held that rapid thawing would cause death after freezing but slow thawing would enable plants to survive. He cited examples of saving plants by thawing them in cold water. Müller-Thurgau (1880) compared the rate of thawing in air and in water of the same temperature and found that the rate of thawing in water was greater than the rate in air. A wide series of plants were tested for injury after slow thawing and after rapid thawing. Some plants showed typical spots of frost injury but were not killed, others showed no injury, and still others were killed outright. Müller-Thurgau (1880) concluded that rate of thawing was not closely correlated to survival after freezing, and that plants that would be killed by rapid thawing could not be saved by slow thawing.

Müller-Thurgau (1880) figures ice crystals in his first paper and also "Eisdrüsen" or ice glands—centers of crystallization. He also gives a method for determining the amount of water formed into ice. He concludes that there can be no freezing to death without first ice formation. Death does not precede freezing but follows it. He also gives extended figures on the winter temperatures of the north and south sides of trees, and shows the alternate freezing and thawing to which trees are subjected. This last phase of his work is important in the present considerations for the oak borers are exposed to the same conditions as the trees which they inhabit.

Müller-Thurgau (1880, 1886) found that plant sap froze at higher temperatures than the whole plant. He explains this higher freezing point on the basis of capillarity and structure of protoplasm. The intact plant is able to hold its water and prevent part of it from freezing. Alto-

gether these papers of Müller-Thurgau form one of the most important contributions to plant freezing and hardening. He also made some general observations on freezing in animals. On account of the importance of the study of tree temperatures in the study of the oak borer group, the following work is quoted. Emerson (1889) studied the temperatures of tree trunks in Nebraska. Squires (1894) and later Harvey (1923) studied the temperatures of trees in Minnesota. Graham (1920, 1922), made a study of tree temperatures with special reference to the maximum temperature endured by insects living under the bark. The influence of the color of the bark on the temperature of the cambial layer was stressed by both Graham and Harvey. Black bark has a higher temperature at a given air temperature than white bark. In winter, according to Harvey, there may be as much as 25°C. difference between the temperature of the north and of the south sides of trees. Alternate freezing and thawing of a living cambial layer is produced by alternation of sunlight and shadow when a cloud passes.

II. LITERATURE ON THE EFFECTS OF LOW TEMPERATURE ON ANIMALS WITH SPECIAL REFERENCE TO INSECTS

The progress of low temperature studies on insects has not been as rapid, nor has the quantitative aspect been emphasized as much as has been the case in plant physiology. The large economic losses from tender plants and the consequent desire to develop hardy varieties have had no counterpart in applied entomology, with the exception of some work concerning the insecticidal effects of low temperature over given periods of time.

The problem of hardiness in insects is essentially a part of the problem of hibernation. Animals that live in cold cli-

mates must adapt themselves to the conditions as they are, or avoid these conditions by migration to warmer or better protected places. This paper deals with animals that are so situated that they cannot avoid the low temperatures of winter but must take the temperature just as it is.

Allied to the problem of hibernation is the question of heat regulation which plays an important part especially in the hibernation of mammals. Rasmussen (1916) gives a summary of the different theories of hibernation. During hibernation homoiothermal animals become poikilothermic. In this latter state they are able to endure cold and starvation which under other conditions would be fatal. The hibernation of mammals may throw some light on the allied problem, the hibernation of insects. Low temperature, high concentration of carbon dioxide, and periodicity, were the chief factors proposed as causes of hibernation. An incompletely homoiothermic mechanism was associated with hibernation. The influence of low temperature on the production of a state of lethargy holds for insects as well as other animals. Periodicity has been emphasized by many workers. The question of a heat regulating mechanism is not fully settled, but there is some evidence from the work of Newport (1837), Bachmetjew (1901), and Pirsch (1923) that insects do have a slight control of their bodily temperatures under different environmental conditions.

The earliest literature on insect hibernation is gleaned from collectors' notes and simple observation that insects are found at low temperatures or do pass the winter out-of-doors. These notes will be passed over, as they do not contribute vitally to the subject in hand.

Aristotle knew that insects hibernated, but did not seek an explanation for this phenomenon.

One of the most striking characteristics about the state of hibernation is its periodicity. Even the name suggests this characteristic. Kirby and Spence (1818) view the phenomenon of hibernation as periodic, although this is not explicitly stated. The action of cold it is pointed out is not sufficient to account for the state of hibernation. Insects in hibernation, it is noted, are able to withstand extremes of low temperature, fatal to them in the active state. The statement is also made that insects frozen as solid as a block of ice can live after being thawed out, but that some insects die from the effect of cold before the freezing point is reached. Hibernation is looked upon as a provision against starvation at a time when the food of insects, whether herbivorous or carnivorous is no longer obtainable.

Baumberger (1917) makes much of the factor of periodicity. Hibernation, according to this author, is essentially a rhythmic phenomenon. It does not occur in tropical insects and is not well fixed in animals more or less protected from winter temperatures. The most fixed and the most periodic hibernation periods occur in animals exposed to winter temperatures habitually.

The meaning of the state of hibernation especially in regard to change or lack of feeding in this state was observed experimentally by Reaumur (1740) and by Huber (1792) in bees. Bees were observed to be active inside their cluster throughout the winter. Réaumur observed that less food was eaten by a hive kept in the cold than one kept in a warm place. Clustering, according to this author, was a manifestation of torpidity. Huber considered that the winter cluster was not the result of torpidity but rather a means of avoiding torpidity by keeping the temperature high.

The state of lethargy in caterpillars was observed by Vaudoner (1827). He noted especially its essential periodicity and observed that this state was not due entirely to lack of food or to low temperatures. Vaudoner's work has been largely overlooked by later biologists. Scudder (1889) found that some caterpillars went into a state of lethargy or premature hibernation at midsummer. Others continued feeding till the onset of severe weather. Between the state of hibernation and activity were shorter and less completely passive periods in the life of some caterpillars. The idea of hibernation as a comparative state rather than an absolute state is here expressed though not explicitly. This idea will reappear again when the subject of cold resistance is taken up. Hibernation of partial broods is considered by Scudder as a means for preserving the species. Thus if part of a group of feeding caterpillars go into a state of lethargy at one time and part at another, the chances for the survival of the species is better.

Associated with hibernation are other low temperature effects such as the freezing point of insects under different conditions, undercooling, hardiness, and lowered rate of metabolism. The rate of metabolism will not be discussed in this paper except in so far as it bears directly on the general problem of hardiness.

The observations of cold resistance in insects are scattering and often indefinite. A certain insect seen on a cold day, or revived after being exposed to winter temperatures, is a common type of observation. However, not all the observations are of this indefinite kind, for Réaumur, who was interested in temperature, was making measurements of the temperatures borne by some little larvae found in wood. Réaumur (1736) placed

small larvae in a freezing mixture of marine salt and water. The larvae were placed in a glass tube and the temperature of the freezing mixture taken. Larvae were able to withstand -8° or -9° Réaumur without perishing. These experiments were performed in the years 1708 and 1709 but were published in his monumental work *Mémoires pour servir à l'Histoire des Insectes*. In this work he also quotes an experiment of Lister who found that insects frozen so hard that they sounded like stones when dropped into a glass survived. This experiment has been requoted many times and has entered into current thought regarding the subject of survival from freezing. The fact of becoming stiff, even hard, may not be a proof that the insect is actually frozen, although workers today as well as in the 18th century, assume the two states to be identical.

The taking of individual temperatures of insects was first accomplished by means of small mercury thermometers. Davy (1826), Rengger (1817), Regnault (1819), and Hausmann (1803) were pioneers in this work. Newport (1837) conducted extensive studies on temperatures of insects of several species and representing four orders. These workers laid the foundation for later work on insect temperature and cold resistance.

'By far the most comprehensive work dealing with the subject of insect temperature up to the present time is the work of Bachmetjew (1901). He summarized the work of his predecessors, performed numerous experiments and formulated conclusions regarding insect temperatures and cold resistance in insects. He used the thermocouple to measure the temperatures of insects and to record freezing points. He emphasized the time rate of cooling or the "Abkühlungs geschwindigkeit" as influencing the vital tempera-

ture minimum, or the lowest temperature at which insects could survive. He also correlated the amount of "sap" present with the freezing point. This term is not quite equivalent to moisture for it represents the difference in weight between a normal insect and a desiccated one. That the weight loss may not be entirely due to water was recognized by Bachmetjew (1899). The size and structure of the cell contents was also recognized by Bachmetjew as correlated with the freezing point. There is one conclusion that Bachmetjew makes with regard to his vital temperature minimum that is difficult to understand. The reaching of the undercooling point for the second time, according to this author, determines death. The undercooling point rather than the freezing point is considered as the critical point. With regard to death occurring at the time of reaching this undercooling point the second time, the data of this author admit of more than one interpretation. About 27 per cent of his results disagree with his conclusion.

Bachmetjew's contributions to the subject of insect freezing can be summed up as follows: (1) the time rate of cooling determines the undercooling point and hence the critical point; the more rapid the cooling the higher the undercooling point; (2) the per cent of "sap" is inversely proportional to the freezing point; (3) the point of death is reached when the insect reaches the undercooling temperature a second time. The lowest undercooling point that was obtained by this author was -15.7°R .

Gueylard and Portier (1916) found that the survival of *Cossus* and *Carpocapsa* on exposure to low temperatures depended upon the season of the year. In winter these larvae were able to survive -20°C . but were killed by that temperature in the spring. In a later paper Duval and

Portier (1921) make further observations on freezing points and emphasize further their periodicity. Another contribution made by these authors is the concept of a secondary freezing point. The first freezing point represents the freezing of body fluid while a lower freezing point of the same tissue represents the freezing of the cell substance itself.

Knight (1922) was able to demonstrate a marked periodicity in the freezing point of the Pentatomid, *Perillus bioculatus*. In the fall this bug gained hardiness and in the spring lost it. Knight considered that the freezing point as demonstrated by the thermocouple method was colloidal in nature. Repeated freezing of the same bug brought the freezing and undercooling points nearer and nearer together, with each successive freezing. This action parallels the setting and melting of gelatine and other colloids where the past history influences present behavior.

Pirsch (1923) in a study of the individual temperatures of honey bees found the freezing point was about -1°C . He tried three bees only as his paper dealt chiefly with other phases of the problem of insect temperatures.

Carter (1925) studied the freezing and undercooling points of the bean weevil *Mylabris obtectus*. He found that the insect when uninjured by piercing with the thermocouple was able to withstand lower temperatures than a pierced insect. He found no correlation between the time rate of cooling and the freezing or the undercooling points. The weevils showed no periodicity during the time studied. Representatives of the stored-products pests that would not be expected to show hardening were chosen for his work in order to simplify the problem.

The relation of water content to the freezing point, cold endurance, and hiber-

nation has been suggested by several authors but definitely worked out by comparatively few. Bachmetjew (1899) emphasized the relation between "sap content" and freezing and undercooling points. The work of Tower (1906, 1910) while open to question in some respects is, however, suggestive. The low water content of hibernating forms is emphasized. Breitenbecher (1910) associated with Tower found that he could bring potato beetles out of hibernation by watering the soil in which they were dormant. Bodine (1921, 1923) has found that hibernating grasshoppers possess a low rate of respiration accompanied by a low moisture content. With the breakup of hibernation the water relations are readjusted to a higher level. Hibernation is essentially a rejuvenating process from the standpoint of basal metabolism. Fink (1925) states that hibernating animals have a low respiratory quotient. The breaking up of hibernation in the codling moth by repeated soakings of the hibernating individuals was reported by Townsend (1924) at the fifth Washington Meeting of the American Association for the Advancement of Science.

Bottazzi and Bergami (1924) reported an irreversible precipitation occurring in ox blood serum when it was cooled to -25°C . They were studying the action of low temperatures upon fluid colloidal systems. Perhaps the most comprehensive work on the relation of water to metabolism is that of Babcock (1912). He studied metabolic water in both plants and animals, and states that during hibernation metabolic water is the source from which animals draw their necessary supplies. The amount of water in hibernating animals is lower than that in non-hibernating animals.

The measurement of the cold resistance

of insects has been dependent upon the measurement of temperature itself and upon the applications of methods of temperature measurement to insect material. The invention of the thermometer in 1714 by Fahrenheit, its perfection by Réaumur, together with the interest in measuring temperatures at that period furthered the study of insect physiology. But there is another method of measuring temperatures, namely the thermo-electric method. Volta in 1801 found that an electric current was set up at the junction of two unlike metals. In 1822 Seebeck, using the newly invented instrument, the galvanometer, measured the E.M.F. set up at junctions of unlike substances and correlated these measurements with temperature change. As early as 1831, Nobili and Melloni were recording the temperatures of insects and other small animals by means of the thermocouple.

III. ORIGINAL EXPERIMENTAL RESULTS

The work of the present writer has dealt with the ability of insects to survive temperatures lower than 0°C . The cold resistance was measured by the freezing and by the undercooling points. By freezing is meant actual crystallization of a given body fluid or tissue accompanied by the giving off of heat. By the undercooling point is meant the limiting temperature below the freezing point of a fluid, to which it can be cooled without freezing.

With the thermo-electric method the freezing and the undercooling points of three groups of insects were taken throughout their normal annual cycle. These ecological groups were, (1) the oak borers, normally exposed to temperature extremes; (2) the aquatic insects never exposed to a temperature lower than 0°C ., and (3) stored-products pests, represent-

ing, supposedly, a tropical or sub-tropical group.

With the oak borers the freezing and the undercooling points were periodic and varied with the seasons. The lowest freezing and undercooling occurred in winter; the highest in summer; with fall and spring determinations intermediate. A marked correlation between the environmental temperature and the insect freezing and undercooling was formed. The species used in this study were larvae of *Synchroa punctata* Neum., *Dendroides canadensis* Lec., *Elater* sp., *Melanotus* sp., *Chrysobothris femorata*, *Romaleum rufulum* Hald., *Elaphidion mucronotatum* Fab. *Lep-tura nitens* Forst., *Arhopalus fulminans* Fab., *Xylotrechus colunus*, Fab., *Graphi-surus fasciatus* Deg., and the adult of *Nyctobates fasciatus* Deg.

A series of freezing and undercooling points of aquatic insects was also made. The genera used were *Enallagma*, *Ischnura*, *Gomphus*, and *Sympetrum* among the Odonata; *Leptocella*, *Phryganea*, and *Neuronia* among the Trichoptera; *Buena*, *Belostoma* and *Notonecta* among the Hemiptera; *Halipus*, *Cybister*, *Coptotomas* and *Dytiscus* among the Coleoptera. Nymphs of the Odonata, larvae of Trichoptera, adults of the Hemiptera and adults of the Coleoptera were used. Determinations were made in February, May, July and September. There appeared to be no periodicity in these insects. There also seemed to be no significant difference between different species, different orders or different stages of development. The mean undercooling of all aquatic insects was 1.52 ± 0.3 , the mean freezing 0.57 ± 0.03 .

The insects infesting stored products exhibited no apparent periodicity but were more variable in both undercooling and freezing than the aquatic group. Three species, *Tribolium confusum*, Duval,

Sitophilus granarius Linn., and *Pyralis farinalis* Linn. were studied with the following results:

INSECT	STAGE	NUMBER DETERMINED	MAXIMUM	MINIMUM	AVERAGE
Undercooling					
<i>Tribolium confusum</i> Duval.....	Adult	200	-6	-1.5	-4.5
<i>Tribolium confusum</i> Duval.....	Larvae	200	-8	-5	-5.6
<i>Sitophilus granarius</i> Linn.....	Adult	200	-14	-2.2	-6
<i>Pyralis farinalis</i> Linn.....	Larvae	500	-7	-4	-6
Freezing					
<i>T. confusum</i>	Adult	200	-4.6	-0.5	-2
<i>T. confusum</i>	Larvae	200	-8	-7.1	-3.6
<i>S. granarius</i> Linn...	Adult	200	-8	-1.4	-2.4
<i>P. farinalis</i>	Larvae	500	-7	-4	-6

The mode of undercooling with *Sitophilus granarius* was -4, of freezing -2. Thus both the mode of undercooling and of freezing differ from the mean. The determinations on this species indicate a highly variable population as regards cold resistance.

Although the oak borer group appears essentially periodic as regards resistance to low temperatures it is possible to alter this character by exposure to suitable temperatures and humidities. Exposure of insects to low temperatures in the summer will start the hardening process. Similarly exposure to high temperatures in the winter time will cause loss of hardness. The results of these experiments would indicate that the freezing point and undercooling is not itself essentially periodic but is a response to a temperature condition that is periodic. Thus

in northern climates the succession of seasons is essentially periodic.

Cold hardiness can be produced experimentally (1) by exposure to low temperature or (2) by dehydration.

Conditions associated with low freezing and undercooling temperatures were studied. The most pronounced feature was found to be the low moisture content. The insects in fully hardened condition have a low moisture content, in non-hardy condition a high moisture content. Periodicity was exhibited in the moisture content. That of *Synchra Punctata* varied from 31.1 per cent in February to 54 per cent in August. With *Dendroides* the variation in moisture content was more marked, from 57.4 per cent to 73.5 per cent. Larvae were baked for four hours at 50°C.

Some experiments were tried in order to determine the nature of freezing. Repeated or multiple freezings were taken on the same insect or tissue. These freezings and undercoolings so taken remained constant and exhibited no hysteresis. Samples of blood taken from the aortae showed definite crystals. Transparent larvae also were seen to have crystals within at the time the freezing point was recorded. The process of freezing in this group was interpreted as crystalloidal. The first or primary freezing point is the freezing point of the blood.

It was found that when the oak borers were in winter condition they could survive freezing. However, on lowering the temperature still further a second undercooling point was found and a second freezing. This secondary freezing point was always fatal. For the oak borer group it was near -40°C. The tissue freezing was not definitely isolated but experiments pointed to the possibility of the tissue being either fat within the cells or nervous tissue.

The problem of survival of insects at

low temperatures was studied in considerable detail with special reference to temperatures below 0°C. It was found (1) that insects not fully hardened were killed when the primary freezing point was reached; (2) in fully hardened insects the primary freezing point was not fatal but there occurred a secondary freezing point that was. Experiments were run to determine the relationship between the freezing point and survival of insects when exposed to low temperatures for as long as twelve hours. It was found that insects with high freezing points were never able to withstand long exposure to low temperatures. However, insects with low freezing points could be killed by long exposure when a short exposure would not be fatal.

With insects not in fully hardened condition the absolute minimum fatal temperature or the lowest at which insects can survive can be defined as the undercooling point. The "vital temperature minimum" of Bachmetjew thus is the absolute minimum fatal temperature for the oak borers throughout the summer, early fall and late spring. During the remainder of the annual cycle, the limit of undercooling is no longer the absolute minimum fatal temperature but the secondary freezing point or some point lower than the primary undercooling must be sought. The secondary freezing point represents the freezing of some tissue other than the blood. One experiment was tried to obtain the freezing point of the nervous tissue. The central nervous systems of fifty larvae were dissected out, placed in a small tube and frozen. The undercooling point recorded was -48°C., the freezing point -45°C.

IV. SUMMARY

Due in part to demand for cold hardy plants and in part to the fact that plant physiology is further developed than

insect physiology, the study of cold resistance in plants has proceeded to a farther stage than the study of cold resistance in insects. From workers in plant physiology we can gain light on certain general physico-chemical problems involved in low temperature studies. The cause of death from low temperature has been considered, (1) as due to direct mechanical injury, (2) water loss through changes in permeability, and (3) precipitation of proteins or other irreversible chemical effect. The development of cold hardness through slow growth, dehydration, or exposure to low temperatures showed that cold resistance is a dynamic rather than a static condition. Finally, the most recent work on plants has emphasized certain chemical and physical conditions of the plant tissues to be associated with cold resistance. These are low water content, efficient hydrophylic

colloids, and proteins not easily precipitated by low temperature.

The study of survival of insects at low temperatures has gone through (1) the observation stage, (2) the qualitative experimental, and is now entering the third stage, the quantitative. Studies on hibernation, on individual insect temperatures, and on heat regulation in insects, have all contributed to the general problem of freezing and survival of insects at low temperatures. Determinations for some insects have thus far been made as to the intensity of low temperatures they can survive, and whether or not they can withstand ice formation in their tissues. Aside from the finding that low water content is associated with cold resistance there yet remain to be discovered the physico-chemical factors associated with or causing cold hardness in insects.

LIST OF LITERATURE

- (1) ARISTOTLE. History of Animals. Tr. by Cresswell. Book VIII, Chapt. XVI, p. 213. London, 1902.
- (2) BARCOCK, S. M. 1912. Metabolic water: its production and rôle in vital phenomena. Wis. Agr. Exp. Sta. Res. Bull. no. 22.
- (3) BACHMETJEV, P. 1901. Experimentelle entomologische Studien von physikalisch-chemischen Standpunkt aus. Leipzig.
- (4) BAUMBERGER, J. P. 1917. Hibernation: a periodical phenomenon. Annals Ent. Soc. Amer. 10: 179-186.
- (5) BODINE, JOSEPH HALL. 1921. Factors influencing the water content and rate of metabolism of certain orthoptera. Jour. Exp. Zool., 32: 137-169.
- (6) ——. 1923. Hibernation in Orthoptera I. Physiological changes during hibernation in certain Orthoptera. Jour. Exp. Zool., 37: 457-475.
- (7) BOTTAZI, F. L. AND BERGAMI, G. 1924. Azione delle basse temperature sui sistemi colloidali liquidi. Arch. d. Sci. Biol. (Naples), 6: 74-93.
- (8) CARTER, WALTER. 1925. The effect of low temperature on *Bruchus obtectus*. Say, an insect affecting seed. Jour. Agr. Res. (In press.) Thesis for M.S., University of Minnesota.
- (9) CHANDLER, W. H. 1913. The killing of plant tissue by low temperature. Mo. Agr. Exp. Sta. Res. Bull. 8.
- (10) DAVY, JOHN. 1826. Observations sur la température de l'homme et des animaux des divers genres. Ann. Chim. et Phys., 33: 180-197, 2 sér.
- (11) DUHAMEL DU MORCEAU, H. L. ET BUFFON, G. L. 1737. Observation des différents effets que produisent sur les végétaux les grandes gelées d'hiver et les petites gelées du printemps. Mem. Math. et Phys. Acad. Roy. Sci. (Paris), 1737: 233-298.
- (12) DUVAL, M. ET PORTIER, P. 1922. Limite de résistance au froid des chenilles de *Cossus cossus*. Compt. Rend. Soc. Biol., 86: 2-4.
- (13) EMBERSON, R. A. 1889. On the internal temperature of tree trunks. Proc. Neb. Acad. Sci., 6: 245-252.
- (14) FINK, DAVID E. 1925. Metabolism during embryonic and metamorphic development of insects. Jour. Gen. Physiol., 7: 527-543.
- (15) GÖFFERT, H. R. 1839. Ueber der Wärme

- Entwicklung in dem Pflanzen und die Schutzmittel gegen dasselbe. Breslau.
- (16) GORKF, H. 1906. Über chemischen Vorgänge beim Erfrieren der Pflanzen. Landw. Veis. Stat., 63: 149-160.
 - (17) GORTNER, R. H. AND HARRIS, J. A. 1914. Notes on the technique of the determination of the depression of the freezing point of vegetable saps. Plant World, 17: 49-53.
 - (18) GRAHAM, S. A. 1920. Factors influencing the subcuticular temperatures of logs. Minn. State Ent. Rept., 18: 26-42.
 - (19) ———. 1922. Effect of physical factors in the ecology of certain insects in logs. Minn. State Ent. Rept., 19: 22-41.
 - (20) GUYLARD, M. ET PORTIER, P. 1916. Recherches sur la Résistance au Froid des chenilles de *Cossus* et *Carpocapsa*. Compt. Rend. Soc. Biol., 79: 774-777.
 - (21) HARVEY, R. B. 1918. Hardening process in plants and developments from frost injury. Jour. Agr. Res., 15: 83-112.
 - (22) HARVEY, R. B. 1923. The relation of the color of the bark to the temperature of the cambium in winter. Ecology, 4: 391-395.
 - (23) ———. 1923. Cambial temperatures of trees in winter and their relation to sun scald. Ecology, 4: 261-266.
 - (24) HAUSMANN, J. F. L. 1903. De animalium exsanguium respone commentatio (Praemio ornata) Hannover.
 - (25) HUBER, FRANÇOIS. 1792. Nouvelles Observations sur les Abeilles. Genève.
 - (26) JOHNSON, EARL S. 1919. An index of hardiness in peach buds. Amer. Jour. Bot., 6: 373-379.
 - (27) ———. 1921. The seasonal march of the climatic conditions of a greenhouse as related to plant growth. Md. Agr. Exp. Sta. Bull., 245: 85.
 - (28) ———. 1923. Moisture relations of peach buds during winter and spring. Md. Agr. Exp. Sta. Bull., 255.
 - (29) KIRBY, WILLIAM AND SPENCE, WILLIAM. 1818. An Introduction to Entomology; or Elements of the Natural History of Insects, 2: 430-465.
 - (30) KNIGHT, HARRY H. 1922. Studies on the life history and biology of *Perillus bioculatus* Fab., including observations on the nature of the color pattern (Heteroptera, Pentatomidae) Minn. State Ent. Rept., 19: 50-96.
 - (31) LIDFORS, B. 1907. Die Wintergrüne Flora, eine biologische Untersuchungen. Lunds Univ. Årsskrift, N. F., Bd. 2, Afd. 2, no. 13.
 - (32) MAXIMOW, N. A. 1912. Chemische Schutzmittel der Pflanzen gegen Erfrieren. Ber. d. Deut. Bot. Gesell., 30: 52-65; 293-305; 504-516.
 - (33) MORREN, CHARLES F. A. 1853. Souvenirs phenologiques de l'hiver, 1852-53. Acad. Sci. Bruxelles Bul. 20: 160-186.
 - (34) MÜLLER-THURGAU, H. 1880. Ueber das Gefrieren und Erfrieren der Pflanzen. Landw. Jahrb., 9: 133-189.
 - (35) ———. 1886. Ueber das Gefrieren und Erfrieren der Pflanzen II. Theil. Landw. Jahrb., 15: 453-610.
 - (36) NAEGELI, C. 1861. Ueber die Wirkung der Frostes auf die Pflanzenzellen. Sitzber. K. Bayer. Akad. d. Wiss. München, 1: 264.
 - (37) NEWPORT, GEORGE. 1837. On the temperature of insects and its connection with the functions of respiration and circulation in the class of invertebrated animals. Phil. Trans. Roy. Soc. London, 127: 259-339.
 - (38) NEWTON, ROBERT. 1924. The nature and practical measurement of frost resistance in winter wheat. Univ. of Alberta, Coll. of Agr. Res. Bull. 1.
 - (39) NOBILI ET MELLONI. 1831. Recherches sur plusieurs phénomènes calorifiques entreprises en moyen du thermomultiplicateur. Ann. Chim. et Phys., 2 sér., 48: 198-217.
 - (40) PIRSCH, GREGOR B. 1923. Studies on the temperature of individual insects with special reference to the honey bee. Jour. Agr. Res., 24: 275-287.
 - (41) PRILLEUX. 1869. Sur la formation de glaçons a l'intérieur des plantes. Ann. Sci. Nat. Bot., S. 5, 2: 125.
 - (42) RASMUSSEN, A. T. 1916. Theories of hibernation. Amer. Nat., 50: 609-25.
 - (43) RÉAUMUR, R. A. F. 1734-1742. Mémoires pour servir à l'histoire des Insectes, 2: 141-147; 170; 5: 667.
 - (44) REGNAULT. 1849. (A note on insect temperatures.) Ann. Chim. et Phys., 3 sér., 26: 517.
 - (45) RENGGER, J. K. 1817. Physiologische Untersuchungen über die thierische Haushaltung der Insekten. Tübingen.
 - (46) ROSA, J. T., JR. 1921. Investigations on the hardening process in vegetable plants. Mo. Agr. Exp. Sta. Res. Bull. 48.
 - (47) SACHS, J. 1860. Crystallbildungen bei dem gefrieren und Veränderung der Zellhaute bei den aufthauen saftige Pflanzentheile. Landw. Vers. Stat., 2: 157-201.
 - (48) SCHAFFNYR, E. 1910. Studien ueber den Einfluss nieder Temperatur auf die Pflanzliche

- Zelle. Mitt. Kaiser Wilhems. Inst. Landw. Bromberg, 3: 93-115.
- (49) SCUDDER, SAMUEL HUBBARD. 1887. The Butterflies of the Northeastern United States and Canada, with special reference to New England, 1: 551-578; 688-693.
- (50) SEEBECK, T. J. 1820. Magnetische Polarization der Metalle und Erze durch Temperatur Differenz. Ann. d. Phys. (Poggendorf), 3 R., 6: 1-20; 133-160; 253-286.
- (51) SEEBECK, T. J. 1822-23. Om Thermoelectricitet. Kiobenhavn. Oversigt., 1822-23: 9-10.
- (52) SQUIRES, R. W. 1894. Tree temperatures. Minn. Bot. Studies, I, no. 26.
- (53) TOWER, WILLIAM LAWRENCE. 1906. An investigation of evolution in chrysomelid beetles of the genus *Leptinotarsa*. Carnegie Inst. Wash. Pub., 48: 245-252.
- (54) ———. 1910. The Mechanism of Evolution in *Leptinotarsa*. Carnegie Inst. Wash. Pub. 263.
- (55) TOWNSEND, M. T. 1924. Water as a factor in the breaking up of hibernation in the codlin moth larvae (Manuscript). Received before 5th. Washington meeting of the Amer. Assoc. Adv. Sci.
- (56) VAUDONER. 1827. Observations sur la lethargie periodique des chenilles des papillons, Euphrosina et Dia. Ann. Soc. Linn. Paris, 6: 374-378.
- (57) VOLTA, ALEXANDRO. 1801. De electricité galvanique. Ann. de Chim., 40: 225-256.





RENNER'S STUDIES ON THE GENETICS OF OENOTHERA

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THERE is only one group among the higher animals and plants that has persistently failed to give genetic results that can easily be interpreted by means of the generally applicable principles. The Evening Primrose (*Oenothera*) has been studied for thirty years, first by de Vries and more recently by a number of other workers; but the results obtained are still quite anomalous as compared with what is known of any other intensively studied organism. The cytological work of Miss Lutz, Gates, Stomps, Boedijn and others has now shown that many of the results are due to the occurrence of triploid, tetraploid, and "trisomic" ($2n + 1$) types; but apart from variations in chromosome number there remains a mass of puzzling data as to the behavior of the 14-chromosome species and "mutant" races.

Oenothera Lamarckiana was long ago shown by de Vries to produce regularly about 2 per cent of "mutant" offspring. About three fourths of these can now be identified as due to extra chromosomes; the remainder appear to be due to heterozygosis in the parent. But if *Lamarckiana* is regularly heterozygous, why does it not produce a still higher percentage of new types—at least 25 per cent—among its offspring? When *Lamarckiana* is crossed to other species of *Oenothera*, F_1 usually includes two distinct types, though both parent species breed nearly true—

and these "twin hybrids" themselves often breed nearly true. Many species crosses in *Oenothera* give different results according to which species furnishes the egg, which the pollen. Finally, the ratios obtained from various mutant and species crosses in the group are variable and are rarely in accord with simple Mendelian expectations.

These and other remarkable peculiarities of the Evening Primrose have been intensively studied in Germany by Professor Otto Renner, and it is the purpose of the present review to show how Renner's work helps to explain the genetic behavior of *Oenothera*.

The first two papers to be considered (1914, 1917a) deal with the problem of the twin hybrids produced by *Lamarckiana*. Renner found that when *Lamarckiana* is self-fertilized, about half the seeds formed are incapable of germination. But when *Lamarckiana* is fertilized by *biennis* or *muricata* (crosses which result in twin hybrids) practically all the seed is viable. Renner therefore assumed that *Lamarckiana* is heterozygous for two gene-complexes, neither of which is viable when homozygous. One of these, called *gaudens*, produces the twin known as *laura*; the other, known as *velans*, produces the twin *velutina*. *Lamarckiana* is then *gaudens-velans*; the inviable seeds are *gaudens-gaudens* and *velans-velans*. The hypothesis accounts for several other facts, such as that *Lamarckiana* may be

reconstituted by crossing *laeta* and *velutina*. Renner further suggested that some of the mutant types were due to exchange of materials between the *gaudens* and *velans* complexes.

Genetic studies (1917b, 1917c, 1918a) showed that the wild species *biennis*, *suaveolens*, and *muricata* are likewise complex heterozygotes—as was also clear from the earlier results of de Vries. Renner has given special names to the haploid gene-complexes of these species and of *Hookeri*, as follows (*Lamarckiana* is included for completeness):

biennis = *albicans*, *rubens* ♀ — *rubens* ♂
Lamarckiana = *velans*, *gaudens* ♀ — *velans*,
gaudens ♂
muricata = *rigens* (*curvans*) ♀ — *curvans* ♂
suaveolens = *albicans*, *flavens* ♀ — *flavens* ♂
Hookeri = ^h*Hookeri* ♀ — ^h*Hookeri* ♂

That is to say, *biennis* produces *albicans* and *rubens* eggs, but only *rubens* pollen; *muricata* produces mostly *rigens* eggs, but a few *curvans*; *Hookeri* produces only ^h*Hookeri* (read haplo-*Hookeri*) eggs and pollen. *Biennis* breeds true because *rubens-rubens* dies, *muricata* because *curvans-curvans* dies, and *suaveolens* because *flavens-flavens* dies. *Hookeri* breeds true because it is homozygous: practically all its seeds are capable of germination, and it gives uniform progenies when selfed.

But why do *biennis*, *muricata*, and *suaveolens* produce only one kind of pollen? This problem was attacked by a microscopic study of the pollen grains themselves (1919a, 1919b). In *Hookeri* the pollen grains were found to be uniform in appearance, and practically all were well filled and capable of germination. In all the other species roughly half of the grains were small and empty—quite obviously not capable of germination. These can not be the grains that carry the gene-complexes (*albicans*, *rigens*) that are absent in the functional pollen, since

such bad grains are present in *Lamarckiana*, where both complexes give functional pollen. I shall discuss the bad grains later. In *biennis*, *muricata*, and *suaveolens* the fully formed and well filled pollen grains were themselves found to be of two kinds, equally numerous. One kind was larger than the other, and staining with iodine showed that the starch grains in the larger kind were more spindle-shaped, those in the smaller more spherical. Only the large grains with spindle-shaped starch grains germinated *in vitro*, and when the pollen was placed on stigmas, sections of the styles showed only spindle-shaped starch grains in the pollen tubes. These grains then represent *curvans*, *rubens*, and *flavens*; the round starch grains are present in *albicans* and *rigens* pollen. These conclusions were fully verified by a study of the pollen grains of hybrids of known constitution. The most intensively studied is *curvi-velutina*, at first called *gracilis* (*Lamarckiana* × *muricata*) = *velans-curvans*. The two kinds of pollen produced agreed in size with the grains of *Lamarckiana* (distinctly larger than those of *muricata*) and with the *curvans* grains of *muricata*. Their starch grains also differed in shape, those of *velans* being more spindle-shaped. Studies of the pollen tubes in flowers fertilized by this hybrid showed that the *velans* grew faster than the *curvans*. The genetic results thus become intelligible; for in the short-styled *muricata* and *biennis* some seeds are fertilized by the *curvans* pollen of this hybrid, while in the long-styled *Lamarckiana velans* alone reaches the eggs. In crosses to short-styled plants *velans* fertilizes more eggs than *curvans*, but if competition is decreased by the use of a small amount of pollen, the percentage of *curvans* rises. We have here, then, an important cause of variable and atypical ratios from

Oenothera hybrids. More important still, the method is available for a direct study of non-functional or poorly functional pollen, so that one no longer feels that assumptions as to the nature of the pollen grains simply beg the question.

The eggs of heterozygotes are also sometimes produced in unequal numbers—notably in the case of *muricata*, which only rarely produces *curvans* eggs. The mechanism at work here has been studied by Renner (1921b). Each ovule of *Oenothera* contains a single diploid megaspore-mother-cell. This cell undergoes two maturation divisions, giving rise to four haploid megaspores. These are separate cells (not merely nuclei in a single cell, as in some seed plants), and are arranged in a row. The two upper megaspores, nearest the micropyle, are sister cells—i.e., they come from one of the two cells produced by the first maturation division; the two lower megaspores, nearest the chalaza, come from the other product of the first maturation division. If, as seems probable, the first division is the reduction division, the two upper cells are alike in genetic constitution, and are different from the two lower cells. In *Hookeri* Renner found that the uppermost cell regularly developed into the embryo sack, the three lower cells all degenerating. It is evident that in this case, where all the megaspores are genetically alike, the upper cell has an advantage due to its position alone, and as a result of that advantage it succeeds in growing at the expense of its companions, until it comes to fill the entire space within the nucellus. In the ovules studied, the same result was found for *Lamarckiana*, as was to be expected; for *Lamarckiana* produces both *velans* and *gaudens* eggs, often in nearly equal numbers. But in *muricata* the uppermost cell gave rise to

the embryo sack in only about half of the ovules. In the other half the lowermost cell grew faster than the other three, and ultimately came to be the only one present. Evidently in half the ovules the *rigens* complex is segregated to the upper cells, and the usual course of events follows. In the other half of the ovules, *curvans* goes to the upper cells, *rigens* to the lower; and in this case the *rigens* cells have a sufficient inherent advantage over the *curvans* so that they usually succeed in overcoming the disadvantages of their position. The genetic results show that the various complexes can be roughly classified according to their "strength" in such competition between megaspores. *Curvans* is always "weak," *velans* is always "strong." *Rubens* never succeeds in competition with *velans*, is usually unsuccessful against *albicans*, but never fails against *curvans*. It is clear that these results can not be explained by assuming the presence of egg lethals; but the competition interpretation does work out consistently.

Another complication cleared up by Renner (1922, 1924) is the behavior of the chloroplasts in *Oenothera* hybrids. It was shown by de Vries and others that species hybrids in this group sometimes are white or pale green, or are mosaics of green and pale regions. *Hookeri* ♀ × *Lamarckiana* ♂ gives two kinds of hybrids, ^h*Hookeri-gaudens* and ^h*Hookeri-velans*, which are both normal green in color. The reciprocal cross, *Lamarckiana* ♀ × *Hookeri* ♂, gives a ^h*Hookeri-gaudens* like the preceding one; but the ^h*Hookeri-velans* is either pale green or mottled pale green and dark green. Renner shows that this result is explicable on the assumption that the plastids of *Lamarckiana* are not able to develop their normal amount (or kind) of chlorophyll in the presence of ^h*Hookeri-*

velans (or ^h*Hookeri*-^h*Hookeri*) nuclei. Some of the hybrids, however, obtain a few plastids from the *Hookeri* pollen tubes, and these develop into the occasional dark green patches. The hypothesis was tested by many crosses. The ^h*Hookeri-gaudens* sisters of the mosaics, when selfed, give rise to homozygous *Hookeri* plants, which are pale green, without any patches. But if the same ^h*Hookeri-gaudens* is fertilized by pollen from *Hookeri*, some of the resulting homozygous *Hookeri* have dark green patches, evidently because *Hookeri* plastids have been introduced by the pollen. In certain combinations involving other species both of the reciprocals are mosaics. *Rubens-curvans*, for example, is white when the plastids come from *biennis*, green when they come from *muricata*. The F₁ plants are white with a few green patches when *biennis* is the mother, green with pale spots when *muricata* is the mother. Such mottled plants often produce branches that are entirely of the dark green color characteristic of the paternal plastids; in such cases the flowers on these branches behave genetically also as though they had only paternally derived plastids. In general, the results make it clear that the development of chlorophyll depends on the constitution of the nuclei and also on that of the plastids themselves. The plastids of each species have characteristic properties, which are transmitted as such and are not at all affected by the nuclear constitution. A plant may have *muricata* plastids and transmit them to its offspring, even though its nuclei do not contain either *rigens* or *curvans*. These results serve to explain the occurrence of white and pale green inviable seedlings, and to clear up another cause of differences between reciprocal hybrids—besides being in themselves perhaps the most instruc-

tive cases of plastid inheritance yet recorded.

Renner has consistently aimed at the analysis of the gene-complexes of *Oenothera* into their component Mendelian units. His most recent paper (1925) gives a summary of the results so far obtained in this direction. As early as 1917 he suggested that the complexes do sometimes interchange materials, and that many of the mutant types of de Vries and others are due to such interchanges. *Gaudens*, for example, carries a recessive gene for dwarfness, and this occasionally goes over to *velans*, giving a *velans*-plus-dwarfness or "*nanovelans*" complex. There results the familiar mutant type *nanella* = *gaudens-nanovelans*. The pale flowered type *sulfurea* of *biennis* is produced in a similar way; and it is probable that many of the other types of *Lamarckiana* (such as *deserens*, *decipiens*, and *blandina*) are also due to exchanges of material between opposing complexes.

Renner has especially studied the various hybrids of the five species that he has worked with. Practically all the possible combinations of the eight primary complexes have been obtained, and their offspring studied. (*Albicans* and *rigens* never function in pollen, and therefore can not be obtained together. *Rubens* and *gaudens* have a common zygote lethal, so that *rubens-gaudens* dies.) Some of these (e.g., *curvans-flavens*, *rigens-velans*, ^h*Hookeri-rigens*) give a distinctly higher percentage of new combinations than do the original species. The data do not as yet suffice to show in detail how the various complexes are related in terms of genes; but several results are clear, and there are a large number of other partial analyses. I shall here only point out a few of the more striking results. The *curvans* complex is shown to carry two distinct and separable zygote lethals.

The zygote lethal of *flavens* may be replaced by a viable allelomorph from *rubens*, *rigens*, or *gaudens*, so that plants homozygous for practically the whole *flavens* complex may be obtained and studied. The gene R, for red nerves, acts as a zygote lethal (as shown by Heribert-Nilsson). It occurs in some races of *Lamarckiana*, and is there independent of the *velans-gaudens* complexes in inheritance. It is sometimes present in *rigens*, and is always present in *rubens* but never in *albicans*—i.e., in *biennis* it is completely linked to the rest of the genes composing the two complexes. In *curvans-velans*, when R is present and was received from the *Lamarckiana* parent, it is completely linked to *velans*—though in *Lamarckiana* it was independent of *velans*.

Renner discusses three possible interpretations of the interchanging of elements between complexes.

1. Linkage, due to the genes concerned all being carried in the same chromosome pair. This interpretation is accepted by Renner as accounting for at least part of the results—i.e., some of the genes concerned probably do show linkage of the ordinary type. But an attempt to account for all the results on this basis meets with difficulties—chiefly in that at least three (perhaps four) loci may be completely linked in some combinations, whereas in others they may be completely independent. The chromosome would therefore have to be extremely long (as measured by crossing over), and would also have to be subject to very striking variations in crossing over.

2. The genes concerned are really independent in inheritance, but nearly all the new combinations of them are inviable. It seems certain that many of the new combinations are inviable, and the empty pollen grains referred to above are probably mostly to be attributed to this cause, as are also the numerous inviable female gametophytes. But it is easy to show that there is not enough elimination of gametes and zygotes to account for the number of different genes for which the plants are heterozygous. It follows that the parental combinations are produced in larger numbers than are most of the new combinations.

3. Chromosome linkage. The cytological observations of Cleland suggest that the chromosomes are not segregated at random at the reduction division; and Renner is inclined to think that in this direction is to be sought a still further special complication of the *Oenothera* situation. He even outlines a tentative arrangement of the genes and groups of genes separated from the various complexes among five of the available seven pairs of chromosomes. This arrangement is intended only as a working hypothesis; but it should be possible to test it cytologically and by the use of trisomic types.

In the present review I have only attempted to give the general results and a few special examples. In the original papers (especially 1919b and 1925) the reader will find an astonishingly large amount of data, and abundant evidence that Renner has spared no pains to put his hypotheses to every available test.

LIST OF LITERATURE

- RENNER, O. 1914. Befruchtung und Embryobildung bei *Oenothera Lamarckiana* und einigen verwandten Arten. *Flora*, 107: 115-151.
- 1917a. Die taube Samen der Oenotheren. *Ber. deutsch. bot. Ges.*, 34: 858-869.
- 1917b. Versuche über die gametische Konstitution der Oenotheren. *Zeits. ind. Abst. Vererb.*, 18: 121-294.
- 1917c. Artbastarde und Bastardarten in der Gattung *Oenothera*. *Ber. deutsch. bot. Ges.*, 35: 21-26.
- 1918a. Weitere Vererbungsstudien an Oenotheren. *Flora*, 111: 641-667.
- 1918b. Bemerkungen zu der Abhandlung von Hugo de Vries: Kreuzungen von *Oenothera Lamarckiana* mut. *velutina*. *Ber. deutsch. bot. Ges.*, 36: 446-456.
- 1919a. Über Sichtbarwerden der Mendelschen Spaltung im Pollen von Oenotherabastarden. *Ber. deutsch. bot. Ges.*, 37: 129-135.
- 1919b. Zur Biologie und Morphologie der männlichen Haplonten einiger Oenotheren. *Zeits. Bot.*, 11: 305-380.
- 1921a. Das Rotnervenmerkmal der Oenotheren. *Ber. deutsch. bot. Ges.*, 39: 264-270.
- 1921b. Heterogamie im weiblichen Geschlecht und Embryosackentwicklung bei den Oenotheren. *Zeits. Bot.*, 13: 609-621.
1922. Eiplasma und Pollenschlauchplasma als Vererbungsträger bei den Oenotheren. *Zeits. ind. Abst. Vererb.*, 27: 235-237.
1924. Die Scheckung der Oenotherabastarde. *Biol. Zentralbl.*, 44: 309-336.
1925. Untersuchungen über die faktorielle Konstitution einiger komplexheterozygotischer Oenotheren. *Biblioth. Genet.*, 9. 168 pp.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

A PHILOSOPHICAL INTERPRETATION OF NATURE

Being a review of *Science and the Modern World: Lowell Lectures*, 1925, by Alfred North Whitehead, Fellow of Trinity College in the University of Cambridge and Professor of Philosophy in Harvard University. New York (Macmillan), 1925. \$4.00.

By Lawrence J. Henderson, Harvard University

This book of Lowell lectures, in the author's phrase, "embodies a study of some aspects of Western culture during the past three centuries, in so far as it has been influenced by the development of science." It describes an epoch during which, on the whole, older interpretations of life, of the world, and of nature have steadily lost ground to materialism and to a mechanistic philosophy based upon physics. The main ideas which have guided this continuous evolution of modern thought are developed in broad outline, from the standpoint of the specialist in theoretical physics, but with an ever present sense that nothing can be more important than a dominant philosophy. Such, in substance, is White-

head's modest description of a work which is also an important and original contribution to philosophical thought, which may possibly be destined to revolutionize our interpretation of nature, and which, at any rate, goes far to replace materialism by a philosophy of organism. The present state of science and of thought, and the search for a way out of present difficulties through recognition of organization as the most concrete reality of nature, make up the real subject matter of this book. For this reason biologists and naturalists will find here the clear expression that they have long needed of ideas which they themselves can neither escape nor, without aid from physics and philosophy, sharply define.

The book opens with a discussion of the fascinating and difficult problem of the origins of the modern scientific mind. "The most intimate change in outlook which the human race had yet encountered" commenced quietly with the appearance of a new interest, or a new intensity of interest, in the bearing of irreducible, stubborn facts upon generalizations. It was carried forward because men who were fired by a strong, unyielding faith that everything exemplifies general principles, and that these can be

known, also became "apt for the state of imaginative muddled suspense which precedes successful inductive generalization."

This phrase must not be passed by without remark, for I feel sure that no experienced investigator can read it and remain unmoved. Its self-evident truth shows how far the problem of scientific method is psychological, and, to me at least, it seems a well nigh perfect statement of the *differentia* of the man of science at work.

From another standpoint Whitehead sees the beginning of modern science as an anti-intellectualist movement arising from the perception that nature is more subtle than the human reason. This is a reaction against the rationalism of mediaeval theology, yet modern faith in the possibility of science remains as an unconscious derivative therefrom. Again, modern science could not be what it is without a vision of the order of nature as akin to the remorseless inevitableness of Fate in Greek tragedy.

Another almost independent ingredient of modern science is noted in the rise of Naturalism in the later Middle Ages, especially in decorative sculpture. This precedes and is the source of the scientific interest in objects for their own sake.

Once established, modern science soon experienced the formative influence of mathematics. The Arabic notation, algebra, logarithms, analytical geometry, and the infinitesimal calculus were the necessary instruments of the great achievements of the incomparable seventeenth century. Its men of genius have stamped physics with the mark of mathematics, and physics determines the character of the century. In Whitehead's opinion "a brief, and sufficiently accurate, description of the intellectual life of the European races during the succeeding two

centuries and a quarter, up to our own times, is that they have been living upon the accumulated capital of ideas provided for them by the genius of the seventeenth century." No doubt an exception to this statement is to be made in favor of the idea of evolution. Most of these ideas we owe to that development, perhaps the greatest in the history of the intellect, which began with Galileo and ended with Newton, including also the labors of Descartes and Huyghens. It is all summed up in Newton's *Principia*.

This development provided posterity with a blank form of a universe, which remained to be filled up. It produced the concepts of inertia, of mass, of an isolated system, of conservation and of force, and it led to the secure foundation of the mechanistic theory of nature, "which has reigned supreme ever since the seventeenth century. It is the orthodox creed of physical science. Furthermore, the creed justified itself by the pragmatic test. It worked. Physicists took no more interest in philosophy. . . . But the difficulties of this theory of materialistic mechanism very soon became apparent. The history of thought in the eighteenth and nineteenth centuries is governed by the fact that the world had got hold of a general idea which it could neither live with nor live without."

The difficulty is most easily seen in the inconsistency of our mechanistic philosophy, which enthrones physical causation as supreme, with our political and social judgments, which always imply final causes. As Whitehead remarks, "it is not popular to dwell on the absolute contradiction here involved." This leads to the problem of freedom and to Mill's famous doctrine, which is promptly dismissed with the scant courtesy which it deserves. Thus we reach a position which has often been reached before, but which

has always seemed a cul-de-sac. Countless biologists during the last half century have found themselves in the ridiculous situation, from which there was no escape, of paying lip-service to the mechanistic theory which was never of the slightest usefulness or relevancy in their researches. The difficulty has always been that the mechanistic theory was known to work; in fact it often worked quite as well in bio-physics and bio-chemistry as elsewhere. Yet in morphology, cytology, genetics, ecology, and similar sciences it has been mainly irrelevant.

Meantime, however, a change has come over physics. As a result of the rise of modern atomism, of the theory of relativity and of the quantum theory, the solid foundations have melted away, and it is not yet possible to judge of the new foundations which must some day replace them. What then "is the sense of talking about a mechanical explanation when you do not know what you mean by mechanics." No one who sees clearly can fail to perceive that the breaking up of the classical philosophy of physics must infallibly release biology from a bondage which has in the past done much good and much harm. The old sanctions, in truth, no longer hold; but, as always, men who have formed the habit of respectful obedience to the law do not know when they have been set free. The news must be spread, and other sanctions, better suited to its needs, must be set up by an independent biology; only there must be no return to vitalism.

At the very moment when the old concepts of science—time and space, matter and motion, energy, mechanism and many others—have lost their intelligibility, physiology, following the path which Claude Bernard mapped out, has finally attained a position of independence. This

result, though indirectly favored in many respects by the orthodox scientific philosophy of the past half century, has also been retarded by it. In particular, the doctrine of organism has had to win through on its merits. A relatively concrete interpretation of nature, it has met persistent opposition from "the intolerant use of abstractions [which] is the major vice of the intellect."

In the concept of organism, Whitehead believes that he has found a means to construct a philosophy which shall replace mechanism. Consider, for instance, the quantum theory and the atom. The electron is a vibratory entity; in his view it may probably be regarded as an entity *constituted by* the vibrations. Hence its path in space can only be represented by a series of discrete, discontinuous positions, and, on this view, it could not even exist except as a periodic system. So far as we know, its existence at an instant is no more conceivable than the existence at an instant of a musical note. The significant thing about it is pattern, not substance; its essence seems to be its characteristic pattern; in short, it is an organism. (This, of course, implies a definition.) No doubt if we are ever successfully to think of electrons in this manner, we must overcome some of our deeply ingrained habits of thinking. Especially we must get rid of the most fundamental of all our scientific concepts, that nature is made of matter "which has the property of simple location in space and time" and "that the world is a succession of instantaneous configurations of matter."

Here it should be pointed out that such a task, immensely difficult in itself, will be made still more difficult because the classical methods of physics will probably long remain the most economical for disposing of the vast stores of accumulated

knowledge. Also there is almost certainly a psychological predisposition in favor of classical materialism, which, I think, makes it seem the most 'reasonable' philosophy to 'reasonable' men. On this account, and because of its marvelous power, I cannot escape the conviction which, though not expressed, is probably also Whitehead's view, that, through all changes of philosophical opinion concerning its truth, the classical theory is likely forever to remain in use as one of the indispensable means of thinking about physical phenomena.

But in spite of its efficiency, in spite of its acceptability, Whitehead believes that, even from the standpoint of naive realism, materialism "is quite unbelievable. This conception of the universe is surely framed in terms of high abstractions and . . . we have mistaken our abstractions for concrete realities." The criticism seems to be that scientific materialism involves, and must involve, the error which may be called "the fallacy of misplaced concreteness." Therefore the interpretation of nature must be recast and founded upon the concept of organism. For such a philosophy, process is the concrete fact; organism itself is process; and nature is an organic structure of evolving processes. "Nature exhibits itself as exemplifying a philosophy of the evolution of organisms subject to determinate conditions." Here an organism is correlative with what is a bit of matter from the standpoint of materialism.

His doctrine, Whitehead calls the theory of organic mechanism. It aims to be an objectivist philosophy, and to take account at once of the needs of natural science and of the nature of our concrete experiences. In spite of its difficulty, it is a form of naive realism and is rooted in naive experience. In this respect his reference to poetry is significant, and, I

believe, reassuring. In particular, the theory thus emphasizes the final elimination of the doctrine of primary and secondary qualities, which has always been one of the scandals of classical materialism.

Nature, being evolutionary, is characterized by emergent "*events*." The event is a transitory unity possessing value; "it is the ultimate unit of natural occurrence;" but it is no independent entity, for this, on the organic theory, is impossible. Every event is (prehensively) related to all other events, and these relationships are internal, that is to say constitutive.

The concrete enduring entities of the world are organisms. In them the parts, even though themselves organisms, are influenced by the plan of the whole. This is true both within and below the biological sphere. "In the case of an animal, the mental stages enter into the plan of the total organism and thus modify the plans of the successive subordinate organisms until the ultimate smallest organisms, such as electrons, are reached. Thus an electron within a living body is different from an electron outside it, by reason of the plan of the body."

But the pattern of an organism does not changelessly endure. There is a cyclical, rhythmic and recurrent aspect to all endurance which may be expressed by the word "reiteration." Perhaps the harmony or stable pattern of vibratory periods among its constituents is, at the very bottom of the organic scale, in the proton and the electron, the clue to the stability of the organism, and also to adaptation to the environment.

To continue the analysis would lead deep into the fields of metaphysics and of the modern theory of atomic structure, for this work includes the sketch of a large fragment of a new metaphysical system, founded on the most recent

scientific thought and speculation. It is a system novel in itself, and peculiarly important because informed by the knowledge and experience of a professional mathematician and physicist. Since Leibniz there has been no similar approach to philosophy. Perhaps for this reason there are in Whitehead's speculations certain affinities with Leibniz. It is not a question, however, of a common philosophical position. On the other hand, there may be found in Lachelier's essay on Induction, and perhaps in the writings of Cournot, views on one philosophical question which are very close to those here set forth. It is also not uninteresting to note the contrast with Fechner's "Cosmorganic" hypothesis, which no doubt developed from a vague perception of the difficulties which Whitehead has clearly analyzed. But, in spite of physical origins, and the pervasive physical and mathematical coloring with which this work is imbued, the main affinities of Whitehead's central hypothesis are biological. The background that one wants in order to have a setting, within which Whitehead's theory may be clearly seen and closely scrutinized, with no sense of discomfort or constraint, is perhaps best afforded by the biological works of Aristotle and by the theoretical physiology of Claude Bernard. The writings of J. S. Haldane present a related hypothesis, and theoretical ecology also involves similar concepts.

The book contains, among other things, an excellent condensed statement of the larger features of the history of modern science. Some of the historical judgments are of great importance, and there are frequent shrewd explanations of what has really gone on beneath the surface. There are also several chapters devoted to the discussion of philosophical problems which, though important from the stand-

point adopted by the author, bear but slightly upon biology. Many references will be found to general history and to literature.

Partly because of the lecture form, and also on account of the all inclusive subject matter, the book is somewhat disorderly. But it is beautifully written and abounds in profound, wise, and witty remarks, a few of which have been quoted in this review.

No doubt the real cause of a certain lack of unity in the exposition lies deeper. The author is, manifestly, still engaged in working out his theories into what promises to become a complete philosophical system of "organic mechanism." He has now provisionally consolidated the positions to which he has thus far attained. But he is still pressing forward, and, until the enterprise has been completed, there can be neither time nor opportunity for a formal and exhaustive discussion.

It is impossible to foretell what the fate of this system is to be. I can only say that I seem dimly to perceive in it, for the first time, the possibility of escape from the difficulties that have produced the conflicts between mechanism and vitalism, and between freedom and determinism. But here hope has been so long deferred that it is natural to be a sceptic. Meanwhile this sketch of a new philosophy may well suffice to restore and to expand our vision of the scope of biology. Like every other human enterprise, biology needs to be understood as something which is valuable in itself and which is not secondary to other enterprises, but the equal of any. As an "event," in Whitehead's sense, biology acquires just this kind of value. But it also now appears as the science which approaches nearest to the concrete enduring realities of the world. Thus, to the biologist, this book is so important that we may not yet

venture to estimate its importance. One thing is certain; for the first time since modern science gained control of modern thought, a philosophical interpretation of nature has appeared which is based

upon a master's knowledge of physical science, and which assigns to the fact of organization that position in a thoroughly comprehensive scheme of things, to which biologists know that it is entitled.

BRIEF NOTICES

EVOLUTION

SCIENCE, RELIGION AND REALITY.

Chapters by Arthur James, Earl of Balfour; Bronislaw Malinowski; Charles Singer; Antonio Aliotta; Arthur S. Eddington; Joseph Needham; John W. Oman; William Brown; Clement C. J. Webb; William Ralph Inge.

The Macmillan Co.

\$2.50 6 x 8½; 396 New York

This book is a valuable contribution to the discussion of the old problem of the conflict between science and theology. The distinguished contributors are all philosophically minded persons of high technical competence in the fields with which they deal. Dean Inge's concluding chapter is a fine piece of clear thinking. Witness to this statement is borne by the following quotation, which is commended to the attention of American scientists and American theologians equally:

"There are at least three positions between which the Church may make its choice. It may condemn modern astronomy as impious and heretical, as the Inquisitors and the Reformers agreed in doing. Luther denounced Copernicus as a fool who dared to contradict the Bible, 'an upstart astrologer who dared to set his own authority above that of Holy Scripture.' Melancthon thought that those who set forth such theories must have no sense of decency; and Calvin asked, 'Who will venture to place the authority of Copernicus above that of Holy Scripture?' The Roman Church

has lately condemned the doctrine of evolution in terms not less stringent than these. This is one possible policy. It declares that there can be no truce between science and religion till science has renounced its errors and accepted the authority of the Church.

"A second policy, equally open to the Church, is to admit that these traditional doctrines do not belong to the natural order with which science deals, but to claim that they possess a higher truth, to which science cannot reach. This may be done by regarding these and other dogmas as symbolic of eternal truths, aids to the imagination in forming clear conceptions of revealed truth in a region beyond the compass of our senses. The apologist for tradition who takes this line will not be content to justify the use of symbols. He will point out that science itself is an imaginative construction; that the supposed laws of nature are not derived directly from our observation of the behavior of atoms and molecules; that what are called the assured results of science are the work of the mind upon an abstract view of reality, which neglects the values and qualitative properties of things, and attempts to construct a universe out of mathematics and chemistry. This disparagement of science as incapable of forming any adequate synthesis may be pushed so far as to reach what is called acosmism, the theory which denies the objective existence of the world or universe. The conclusion will then be, that though the dogmas in question

are symbolic, they are much nearer to truth than the scientific laws which pronounce them to be impossible.

"The third policy is to recognise that all theological doctrines which rest upon the geocentric theory must be recast, inasmuch as the results of science are, within their own sphere, unassailable. I do not think I underestimate the seriousness of this step, nor the great difficulties in taking it. But anything, I believe, is better than trying to conceal an open sore which destroys our joy and peace in believing. If we adopt this third policy, we shall be driven to think of God less anthropomorphically, and of heaven as a state rather than a place—a state, too, which is eternal in a deeper sense than that of unending time-succession. But I cannot pursue this subject without transgressing the lines set for writers in this volume.

"If I had any doubts that the religion of Christ can and will weather the storm, or if I had any doubts that it is entirely independent of any false opinions about the nature of the universe, my readers may be certain that I should not have spoken as I have done. If I believed that Christianity stands or falls with a Ptolemaic universe, I should be obliged either to take the painful course of confessing that I have believed and taught all my life a creed which is as outworn as Paganism, or I should do like thousands of others—I should hold my tongue. But I am quite confident that this crisis will be surmounted if the Church has faith and courage, and, above all, the common honesty, to face candidly. Only let us hear no more of clergymen thanking God that theology and science are now reconciled, for unhappily it is not true" (pp. 359-60).

Is it permitted the scientist to thank God that there is at least one theologian

who can think straight and clearly, and has courage?



THE ASCENT OF MAN BY MEANS OF NATURAL SELECTION.

By *Alfred Machin* Longmans, Green and Co.
\$2.75 xx + 325 London and New York

This book attempts to arrive at a reasonable explanation of the evolution of modern civilized man. It is based in the main on a re-examination and re-interpretation of the works of Darwin and Spencer. Spencer's main contribution to the problem is held to be that human nature (man as he is) can only be explained by the theory of his descent from a long line of savage ancestry. Darwin's theory of natural selection in Machin's opinion serves, as nothing else serves, to explain the fitful, spasmodic and extraordinary progress of the human race.

The book is well written and will be a valuable addition to the shelves of any biological library. Unfortunately it has no index.



EVOLUTION IN THE LIGHT OF MODERN KNOWLEDGE.

A Collective Work. Contributors: F. O. Bower, James H. Jeans, Harold Jeffreys, E. W. MacBride, W. M'Dougall, C. Lloyd Morgan, M. S. Pembrey, A. A. Robb, G. Elliot Smith, Frederick Soddy, A. E. Taylor, W. W. Watts, Rev. J. M. Wilson.

D. Van Nostrand Co.
\$7.50 6 x 9; xiv + 528 New York

As is to be expected, the contributions of the thirteen different men who write this book are somewhat uneven in quality. Some reach a high standard of popular scientific writing, while others seem somewhat feeble, or biased, or both. What the book attempts to do is to give

an authoritative statement, by representative British scientific men, as to how the doctrine of evolution now stands after the general upheaval of fundamental theories in the last twenty years. The subjects covered are: Cosmogony (Jeans); the evolution of the earth as a planet (Jeffreys); geology (Watts); biology (C. Lloyd Morgan); botany (Bower); zoölogy (MacBride); physiology (Pembrey); anthropology (G. Elliot Smith); mental evolution (M'Dougall); physics and chemistry (Soddy); time and space (Robb); philosophy (Taylor); the religious effect of the idea of evolution (Wilson). Brief bibliographies follow each chapter, and a good working index completes the book. It can be highly recommended as required reading in any general elementary course on evolution.



EVOLUTION, GENETICS AND EUGENICS.

By *Horatio Hackett Newman*

The University of Chicago Press

\$3.50 $6\frac{1}{2} \times 9\frac{1}{4}$; xx + 639 *Chicago*

This is a new and extensively revised edition of the author's widely used textbook. It is constructed on the scrap-book plan, being composed largely of excerpts from the writings of the principal authorities in the fields covered. Considerable pedagogical skill is shown in the arrangement of the material in this new edition, there having been some changes from the arrangement in the first edition. The additional material of greatest interest is a chapter dealing with the Scopes trial at Dayton, Tennessee. In reading this one cannot avoid a little of the feeling that perhaps if the general plan of the rest of the book had been strictly adhered to, and extensive quotations made from either H. L. Mencken's

newspaper account of the trial at the time, or from the writings on anti-evolutionists of Thomas Henry Huxley—the only professional biologist who ever successfully and admittedly demolished the fundamentalists on their own ground—a more realistic picture of the significance to human thought of the events in Tennessee might have emerged. A short bibliography, an excellent glossary of technical terms, and an adequate index close the volume.



EVOLUTION AND GENETICS.

By *Thomas H. Morgan*

Princeton University Press

\$2.00 $5\frac{3}{4} \times 8\frac{1}{2}$; ix + 211 *Princeton, N. J.*

This is a revised edition of the author's well-known Vanuxem Lectures for 1915-16, originally entitled "A Critique of the Theory of Evolution." A good deal of new material has been added, and the original four chapters expanded to thirteen. While intended for a lay audience, the main problems of evolutionary biology are discussed with a critical vigor which is as admirable as it is unusual in these days. The last chapter on human inheritance is especially to be commended.



THE DOGMA OF EVOLUTION.

By *Louis Trenchard More*

Princeton University Press

\$3.50 $5\frac{3}{4} \times 9\frac{1}{2}$; viii + 387 *Princeton, N. J.*

In this volume a physicist criticizes the work of biologists on the problem of organic evolution from a general philosophical standpoint. Some of this criticism is well founded and well sustained and may be read with profit by any biologist. Much of it is mere special pleading in favor of religious mysticism as a system of philosophy. The book seems

certain to be seized upon by fundamentalists as a valuable source of ammunition for their campaign. It lacks an index.



DIE METHODEN DER PHYLOGENETISCHEN (STAMMESGESCHICHTLICHEN) FORSCHUNG (*Handbuch der biologischen Arbeitsmethoden, Lieferung 177*).

By Heinrich Hugo Kärny

Urban & Schwarzenberg

12, 60 Marks 7 x 10; 290

Berlin

This number of the great Abderhalden Handbook of Biological Technique is strongly recommended to the general biologist. So far as we know, there does not exist in the literature any other book which covers quite the same ground as this in quite so useful a way. What it does is to give a general picture of the philosophy and logic of the methodology of paleontology, as applied to the elucidation of the problem of organic evolution. In doing this it also gives a general picture of what paleontology has accomplished towards the solution of this problem. Some enterprising American publisher might do well to arrange for the translation of this volume, if possible.



GENETICS

EXPERIMENTS IN GENETICS.

By Charles Chamberlain Hurst

The Macmillan Co.

\$16.50 7½ x 10½; xxiv + 578 New York

This magnificent piece of book making by the Cambridge University Press, collects into one volume the more important papers covering the genetic work of the author during the thirty years from 1894 to 1924. Major Hurst was a real pioneer in genetics, having begun his work on the hybridization of orchids under the inspira-

tion of Darwin's *Fertilisation of Orchids* in 1894, before the dawn of the Mendelian era. Except for the interruption of the War he has been actively engaged in genetic researches from that date to the present time. The papers in this book fall into four general groups. The first, consisting of the first four papers, deals with the orchid work. The next twenty papers report the results of Mendelian experiments with various genera of plants and animals, together with genetic studies of a more statistical character in horses and in man. The next ten papers discuss mainly the problems of the application of the principles of Mendelism to the practical breeding of plants and animals, and also to some extent with eugenics. The last two papers have to do with the author's latest researches on the genetics of the genus *Rosa*. It is a useful service to genetics to have these papers, originally published in widely scattered journals, collected in a single volume for reference.



ÜBER VARIABILITÄT, KORRELATIVE BEZIEHUNGEN UND VERERBUNG DER HAARFEINHEIT BEI SCHAFEN.

(*Bibliotheca Genetica*, Band VII.)

By Walter Spöttel Gebrüder Borntraeger

30 Marks 7¼ x 10½; iv + 235 Leipzig
and 8 pp. tables

This extremely thorough and detailed biometric and genetic study of wool deals principally with the following topics: (a) the methods of measuring fineness of wool and the biometric treatment of these measurements; (b) the fineness of the wool of different races of sheep; (c) the correlation between fineness of wool and other morphological and physiological characteristics; (d) the inheritance of fineness of wool, in which section the author describes in detail his experimental work

in crossing Mouflon and Somali sheep with Merinos. There is a bibliography covering five pages. Extensive tables of original data are given as an appendix.



OUR PRESENT KNOWLEDGE OF HEREDITY. (*A Series of Lectures Given at the Mayo Foundation and the Universities of Wisconsin, Minnesota, Nebraska, Iowa, and Washington (St. Louis), 1923-1924.*)
W. B. Saunders Co.

\$2.50 5½ x 8; 250 pp. Philadelphia

The authors and subjects of this series of popular lectures are as follows: Heredity, the general problem and historical setting, by W. E. Castle; the heredity of sex, by C. E. McClung; the inheritance of acquired characters, by J. A. Detlefsen; heredity in relation to cancer, by Maud Slye; the influence of heredity on the occurrence of cancer, by H. G. Wells; eugenics, by M. F. Guyer. The volume contains nothing that is particularly new, but it may be found useful as collateral reading in elementary courses in general biology and genetics.



DIE CHROMOSOMENZAHLEN DER HAUPTSÄCHLICHSTEN GETREIDEARTEN NEBST ALLGEMEINEN BETRACHTUNGEN ÜBER CHROMOSOMEN, CHROMOSOMENZAHLEN UND CHROMOSOMENGRÖSSE IM PFLANZENREICH. (*Bibliotheca Genetica, Band VIII.*)

By Karl Viktor Stolze Gebrüder Borntraeger
9,60 Marks 7¼ x 10½; iii + 71 Leipzig

In a systematic way this treatise reviews the existing literature on chromosomes in the grains, and presents the author's own results in this field. There follows a brief presentation of data regarding chromosomes in the plant king-

dom in general. There is a bibliography of 151 titles. This work will be especially useful to the geneticist for ready reference to this particular aspect of plant cytology.



DIE GENETIK DER KARTOFFEL.

(*Bibliographia Genetica I. 1925.*)

By C. Fruwirth Martinus Nijhoff
2.50 Florins 6½ x 9¾; 48 The Hague

The distinguished plant geneticist, Fruwirth, summarizes critically here the present state of knowledge regarding the genetics of the potato, with an appended bibliography of more than 180 titles. The titles covered are: blossoms and fruit; inbreeding; hybridization; spontaneous variation; grafting; degeneration; and the effect of selection.



GENETIC MONOGRAPH ON PISUM.

(*Bibliographia Genetica II. 1925.*)

By S. J. Wellensiek. Martinus Nijhoff
\$2.60 6½ x 10; 134 The Hague

This volume reviews critically the extensive literature on the classic form of post-Mendelian genetics, the pea. Teachers of biology will find it a useful reference work in spite of the sometimes quaint English. The bibliography includes something over 180 titles.



HEREDITY IN RABBITS AND GUINEA-PIGS. (*Bibliographia Genetica I. 1925.*)

By W. E. Castle. Martinus Nijhoff
\$1.00 6½ x 9¾; 40 The Hague

Professor Castle divides his authoritative review of the present state of knowledge regarding the genetics of rabbits and guinea-pigs into the following sections:

Introduction; origin of the domestic rodents; coat characters of the rabbit; blending inheritance in the rabbit; the inherited characters of guinea-pigs; historical. There is a bibliography of 84 titles.



GENETISCHE UNTERSUCHUNGEN AN MOOSEN. (*Musci und Hepaticae.*) (*Bibliographia Genetica I. 1925.*)

By F. von Wettstein. Martinus Nijhoff
2 Florins $6\frac{1}{4} \times 9\frac{3}{4}$; 38 The Hague

This general review of the genetics of mosses (*Musci* and *Hepaticae*) discusses the material under the following headings: Embryology; genetic investigations; crossing experiments; sexuality in mosses. There is a bibliography covering six pages.



GENETISCH-PHYSIOLOGISCHE ANALYSE DER HETEROSTYLE. (*Bibliographia Genetica II. 1925.*)

By G. von Uebisch. Martinus Nijhoff
2.80 Florins $6\frac{1}{2} \times 10$; 56 The Hague

This is an excellent review of the present state of knowledge of the genetics of heterostylism in plants. The significance of physiological and environmental factors, as well as purely genetic, in the production of this condition are discussed. There is a bibliography of 81 titles.



UNTERSUCHUNGEN ÜBER DIE FAKTORIELLE KONSTITUTION EINIGER KOMPLEXHETEROZYGOTISCHER ÖNOTHEREN. (*Bibliotheca Genetica, Band IX.*)

By O. Renner. Gebrüder Borntraeger
22 Marks $7\frac{1}{2} \times 10\frac{1}{8}$; iii + 168 Leipzig

This valuable summary of an important series of genetic studies is discussed in detail in this number of THE QUARTERLY

REVIEW OF BIOLOGY by Dr. A. H. Sturtevant (*cf. supra*, pp. 283-288).



DIE GATTUNG EPILOBIUM. (*Bibliographia Genetica I. 1925.*)

By Ernst Lehmann Martinus Nijhoff
2.80 Florins $6\frac{1}{2} \times 9\frac{3}{4}$; 56 The Hague

The author deplors the fact that plants of the genus *Epilobium* have not been as much used for genetic studies as the nearly related genus *Oenothera*. That a beginning has been made in this direction, however, is indicated by the fact that his bibliography of the pertinent literature includes over 177 titles. The review includes a discussion of the general systematic and morphological bases for the use of *Epilobium* as genetic material, followed by sections on the natural hybrids in the genus, and the experimental genetic studies which have so far been carried out.



GENERAL BIOLOGY

BIOLOGIE DER TIERE DEUTSCHLANDS. (*Lieferungen 1-6.*)

Edited by Paul Schulze. Gebrüder Borntraeger

Lief. 1, 0.81 Marks 43 pp. Leipzig

Lief. 2, 0.9 Marks 55 pp.

Lief. 3, 1.44 Marks $5\frac{1}{2} \times 8\frac{3}{8}$; 69 pp.

Lief. 4, 1.8 Marks 77 pp.

Lief. 5. 52 pp.

Lief. 6. 64 pp.

These little treatises represent the beginning of a useful enterprise. The *Biologie der Tiere Deutschlands* will attempt to fill the need for a work which will, within moderate compass, set forth in an authoritative way the important facts regarding the general biology of all the animal groups represented in Central Europe. Separate parts will be contrib-

uted by specialists. Judging by the first six parts, the result, if the project is carried through to completion, will be a first-rate general natural history. The groups dealt with in the parts before us, and the authors, are as follows: *Fresh Water Sponges* by Paul Schulze; *Fresh Water Hydroids* by Paul Schulze; *Classification of the Families of Mites Found in Germany* by H. Vitzthum; *Ixodina* by Paul Schulze; *Thysanoptera* by H. Priesner; *Leaf Mining Insect Larvae* by Martin Hering; *Hydracarina* by Karl Viets; *Eriophyina* by Paul Schulze; *Other Acarina* by H. Vitzthum; *Araneina* by U. Gerhardt; *Fish* by A. Remane; *Gastrotricha* by Paul Schulze; *Diptera* by E. Lindner; *Turbellaria* by E. Reisinger. The numbers before us are well illustrated and contain brief but useful bibliographies in each case. According to the dates on the parts before us no number seems to have been issued since 1923. It is to be hoped that so promising an enterprise has not come to grief thus early in its career.



SYLLABUS DER INSEKTENBIOLOGIE. (Lieferung 1.)

Edited by Hans Blunck. Gebrüder Borntraeger
6 Marks $5\frac{1}{2} \times 8\frac{3}{8}$; 136 *Leipzig*

This is the first number of an extremely ambitious undertaking which, if carried through to completion, will be of enormous usefulness not only to entomologists but to biologists in general. What it aims to do is to give a detailed subject index of the data of general biological interest, as contrasted with purely taxonomic interest, in the literature of entomology. An elaborate system of abbreviations and condensations is employed to keep the work within reasonable bounds. We shall watch with the greatest interest the progress of this work. The present number makes a fair beginning

on the *Coleoptera*. The general editorship of Dr. Hans Blunck insures that the work will be done with thoroughness.



THE GROWTH OF BIOLOGY.

By William A. Locy. Henry Holt and Co.
\$4.00 $5\frac{3}{4} \times 8\frac{3}{4}$; xiv + 481 *New York*

This posthumous book by Professor Locy is a valuable addition to the existing manuals on the history of biology. It deals with the history of zoology from Aristotle to Cuvier; of botany from Theophrastus to Hofmeister; and of physiology from Harvey to Claude Bernard. It is in the main written around the lives of the individuals who made the advances in biological science. The book is well indexed and illustrated with 140 text figures. It is distinctly a better piece of work than the author's earlier book, "Biology and Its Makers."



THE BIOLOGY OF POPULATION GROWTH.

By Raymond Pearl. Alfred A. Knopf
\$3.50 $5\frac{3}{4} \times 8\frac{1}{4}$; xiv + 260 *New York*

The results of the author's most recent studies, experimental and statistical, of various aspects of the population problem are recorded in this book. Most of the material has not been published hitherto. There is a bibliography of 165 titles. The topics discussed, after a general introductory chapter having the purpose of orienting the reader in relation to earlier work, are: The growth of experimental populations of *Drosophila*; the indigenous native population of Algeria; the mortality of the native population of Algeria; the birth rate of the native population of Algeria; the influence of density of population on fertility; the differential birth rate and the

population problem; human behavior and the birth rate.



PROCEEDINGS OF THE ANNUAL CONGRESS ON MEDICAL EDUCATION, MEDICAL LICENSURE, PUBLIC HEALTH AND HOSPITALS. *Held in Chicago, March 9, 10, 11 and 12, 1925.*

Press of American Medical Association
50 cents $8\frac{1}{2} \times 11\frac{1}{2}$; 134 *Chicago*

A reprint, in convenient form, of the papers and addresses given at the Congress specified in the title. Teachers of pre-medical biology courses will find it useful in getting the point of view of the medical educator.



OUTLINES OF GENERAL BIOLOGY.

An Introductory Laboratory Manual.

By Charles W. Hargitt and George T. Hargitt.
Lea and Febiger

\$2.00 $5\frac{1}{2} \times 8$; vi + 192 *Philadelphia*

The fifth edition of a well-known laboratory guide for an elementary course in general biology. The chief alteration in this edition is the addition of directions for the study of the flatworms, both free living and parasitic.



DIE ISOPOTENZ ALLGEMEIN
HOMOLOGER KÖRPERTEILE DES
METAZOENORGANISMUS. (*Abhandlungen zur theoretischen Biologie Heft 22.*)

By N. G. Lebedinsky. Gebrüder Borntraeger
3,30 Marks $6\frac{1}{2} \times 10$; iii + 36 *Leipzig*

This small volume deals critically with the somewhat specialized problem of the functional and structural consequences of metamerism. The principal conclusion reached is the one suggested by the title, that generally homologous parts of the body are developmentally isopotent.

HUMAN BIOLOGY

OLD AMERICANS.

By Aleš Hrdlička.

The Williams & Wilkins Co.

\$10.00 $6\frac{1}{2} \times 9\frac{1}{2}$; xiii + 438 *Baltimore*

This book is a detailed account of an investigation which has been carried on by Doctor Hrdlička for the past fourteen years. It presents extensive data to show just what physically, and in some measure also physiologically, the old American stock represents, and what developmental changes, if any, have already been realized in it, and towards what it is tending. By "Old Americans" are meant in general those American whites who have been longest in this country. In fact the term is restricted in the investigation to mean those Americans whose ancestors on each side of the family were born in the United States for at least two generations. The following are the main topics dealt with: an historical sketch of the Old American stock; pigmentation; measurements and morphological observations, which includes a thorough general anthropometric survey of the individual; physiological observations; discussion of certain general problems on the basis of the data; and finally the future American type. In view of the author's position in the anthropological world it is really unnecessary to state that the work has been done with extreme care and thoroughness, and will stand as a permanent anthropological reference work. The book closes with a detailed index, covering 26 pages.



THE HOMICIDE PROBLEM.

By Frederick L. Hoffman.

The Prudential Press

6 x $8\frac{1}{2}$; 106 *Newark, N. J.*

The indefatigable Nestor of American vital statisticians performs once more a

useful service to the student of human biology by bringing together a long series of papers dealing with the statistics of murder, originally contributed to insurance journals which practically never come to the attention of biologists. For the United States he gives detailed records of homicides from 1882 to 1924. In the period from 1900 to 1924 inclusive a vast number of laws intended to make and keep us good have been put upon the statute books of the various commonwealths which compose these United States, as well as upon the records of the doings of the Federal Congress. It is an interesting and grimly humorous fact that the homicide rate per 100,000 of population in 28 of the larger American cities, *doubled* in this period. We are under the impression that students of human biology can obtain this valuable little treatise of Doctor Hoffman's without cost, by application to the Prudential Life Insurance Company of America.



HEALTH CONDITIONS AND DISEASE INCIDENCE AMONG THE ESKIMOS OF LABRADOR.

By Samuel King Hutton. *The Wessex Press*
6 Shillings 7½ x 10½; 74 Poole, England

The author of this much too brief book was for seven years a practicing physician among the pure-blooded Eskimos of Northern Labrador. It is an extremely interesting account of his observations on disease among these people. It constitutes a valuable source for the student of human biology in general, and in particular for the philosophically minded student of the problems of public health. These Eskimos live in a harsh environment, where the struggle for physical existence is an ever-present reality. Natural selection eliminates from 40 to 60 per cent of the population

before the age of 5 is reached, and the survivors are highly adapted to living under the conditions imposed by their particular environment. Space is lacking here to quote many of the detailed results; only three may be mentioned briefly. The author never saw or heard of a case of malignant new growth in an Eskimo. Among the real meat-eating Eskimos he never saw or found any record suggestive of the occurrence of appendicitis. Regarding tuberculosis, he makes the following interesting observation: It is an introduced disease; there is no evidence that it existed as a natural disease among primitive Eskimo tribes. "It is not a widespread cause of death among the Eskimos, but runs very markedly in certain families."



MEDICAL HEREDITY. *Distinguished Children of Physicians (United States, to 1910.)*

By William Browning.

The Norman, Remington Co.

\$4.00 6½ x 9½; 262 Baltimore

This entertaining volume performs a real service to the student of human biology. It provides him with a classified list of American persons who attained some degree of distinction in some field of human activity, and were the children of physicians, the list ending with the year 1910. The fields in which distinction were attained are divided into sixteen general classes, and within each class the names are arranged chronologically by birth date. This list is followed by some 40 odd pages of review and commentary; four appendices; and a general index of names. The book provides a mine of material for the biometrician, not at all exhausted by the rather simple statistical

summaries which are as far as the author himself ventures in this direction. Dr. C. B. Davenport contributes an introduction.



ALLGEMEINE RASSENKUNDE. *Als Einführung in das Studium der Menschenrassen.*

Dr. Walter Scheidt. J. F. Lehmann
33 Marks 7 x 10½; xiii + 585 München

This stately and beautifully printed volume is the first in a proposed large work on *Rassenkunde* undertaken by Dr. Walter S. Scheidt in cooperation with Doctors Gero von Merhart, Richard Thurnwald and Ernst Wahle. This introductory volume will be followed by a series on the anthropology of special races, of which the next announced for publication will deal with the races of Europe and the extra-European Mediterranean races. The six sections of the present volume discuss the following subjects: The idea of race in anthropology and the classification of human races (historical review); inheritance in man; the manifoldness of human characters; selection in man; concept of race in human beings; human inheritance, and racial characters. The book closes with extensive indices. It is a significant addition to anthropological literature, which must be in every adequate library of the subject.



THE NEW AGE OF FAITH.

By John Langdon-Davies.

The Viking Press
\$2.50 5½ x 8½; 255 New York

This book is a counterblast to the writings of A. E. Wiggam, Lothrop Stoddard, Madison Grant and their ilk. The author is stated to be a journalist and popular lecturer. The problem with which the book deals is the significance of the

science of biology, in its modern aspects, for the development and control of human social relations. A rather extreme environmentalist position is emphasized throughout.



THE NATURAL INCREASE OF MAN-KIND.

By J. Shirley Sweeney, with an introduction by William H. Welch.

The Williams & Wilkins Co.
\$4.00 6 x 8½; 185 Baltimore

This book gives an account of a detailed biometric study of the vital index (Birth/Death ratio) of all the populations of the world for which the necessary statistical data are available. An entertaining and historically valuable introduction is contributed by Doctor Welch. There is a bibliography of 86 titles and appendices of the raw statistical data used in the inquiry, which will be useful to other students of the population problem. The book is well indexed, and makes a definite contribution to the much discussed population problem.



CANCER MORTALITY AMONG INSURED WAGE EARNERS AND THEIR FAMILIES. *The Experience of the Metropolitan Life Insurance Company Industrial Department 1911 to 1922.*

By Louis I. Dublin, Edwin W. Kopf, George H. Van Buren.

Metropolitan Life Insurance Co.
6½ x 9½; 104 New York

A detailed analysis of the experience of the Metropolitan Life Insurance Company relative to mortality from cancer. In certain respects the material considerably surpasses in value that which can be derived from official vital statistics. The general conclusions as to the trend of cancer mortality are somewhat

more optimistic than many recent ones have been, which were based upon less adequate material and less careful statistical analysis. The authors are to be congratulated for having produced such an excellent piece of timely bio-statistical research.



ZOOLOGY

THE BIOLOGY OF FISHES.

By Harry M. Kyle. *The Macmillan Co.*
\$4.50 $5\frac{3}{4} \times 8\frac{3}{4}$; xvi + 396 New York

This is a well written and illustrated account, from the point of view of modern biology, of the natural history of fishes. The general topics discussed are: The general characters of fishes; habits in general; migration; development; regulation of the form and structures; economy of the body (1) production and transport of energy, (2) utilisation and emission of energy; variation and differentiation; the genealogy of fishes; distribution of fishes in time and space; adaptations to suit particular conditions; fishes and the web of life; the food question; mental life. A bibliography of some fourteen pages documents the statements in the text. The book closes with a good index.



MANUAL OF INJURIOUS INSECTS.

By Glenn W. Herrick. *Henry Holt and Co.*
\$4.50 $5\frac{3}{4} \times 8\frac{3}{4}$; xxi + 489 New York

This is a thorough, systematic treatise on economic entomology, intended primarily for students of agriculture. The first four chapters are of a general introductory character, and are followed by seven chapters on various methods of control of insects injurious to crops, or in other ways. The remaining chapters of the book deal with the insects injurious to particular crops, taken one by one or in

small homogeneous groups. This plan of arrangement involves a good deal of repetition, but is probably the most useful one for the agricultural student. The general zoölogist will find this a handy reference work.



ZOOLOGIE IM GRUNDRISS. (*Lieferungen 1 und 2.*)

By Walter Stempell. *Gebrüder Borntraeger*
Lieferung 1, 6,60 Marks Berlin

$7\frac{1}{8} \times 10\frac{1}{2}$; xviii + 336

Lieferung 2, 6,90 Marks

These two parts constitute the beginning of a textbook of general zoölogy conceived on broad and inclusive lines. A brief introduction of sixteen pages deals with the underlying ideas and scope of zoölogy; with its different divisions; and finally with its history. Then begins the first main section of the whole work, which discusses the morphology and taxonomy of animals. About 50 pages are given to promorphology, which is taken to mean, in the first instance, the general principles of cytology and histology and, secondly, the ground plan of animal morphology. The remainder of these two parts is taken up with a systematic discussion of the comparative morphology of the different animal groups up to and including the vertebrates. So far as may be judged from these first parts, the work when completed will form a useful and welcome addition to the general textbook literature of zoölogy.



BRITISH BIRDS. Vol. II.

By Archibald Thorburn.

Longmans, Green and Co.

\$5.50 $6 \times 8\frac{3}{4}$; ix + 130 New York

The second volume of this beautifully illustrated handbook of British Birds, of which the first volume was noticed in

No. 1 of THE QUARTERLY REVIEW OF BIOLOGY, deals with six orders, as follows: *Passer.s*, *Picariae*, *Striges*, *Accipitres*, *Steganopodes*, and *Herodiones*. The 48 colored plates in this volume seem even more charming than those in the first volume. While the text is meager in amount it contains many interesting and useful bits of information on habits and life histories.

DIE AMEISENMIMIKRY. *Ein exakter Beitrag zum Mimikryproblem und zur Theorie der Anpassung. (Abhandlungen zur theoretischen Biologie, Heft 19.)*

By Erich Wasmann, S. J.

Gebrüder Borntraeger

9 Marks $6\frac{1}{2} \times 10$; xii + 164 Leipzig

This detailed and highly technical review of the facts regarding the mimicry of ants by their guests, ends on a note of high piety. The wisdom and goodness of God seem to be the chief causal factors concerned with the production of adaptive mimicry, with the principle of natural selection as a very second-rate helper. The less spiritual portions of the book will be found useful for reference.

LABORATORY DIRECTIONS IN GENERAL ZOÖLOGY.

By Winterton D. Curtis and Mary J. Guthrie.

John Wiley and Sons

\$1.50 $5\frac{3}{4} \times 9$; xxxiii + 194 New York

This is a revised and extended edition of similar manuals published at various times since 1912 by the senior author. It represents the accumulated experience of some twenty years development of the beginning course of zoölogy at the University of Missouri. It outlines a splendidly organized elementary course.

A LABORATORY GUIDE IN GENERAL ZOÖLOGY.

By A. Richards. Lea and Febiger

\$1.75 $5\frac{1}{2} \times 8$; viii + 149 Philadelphia

The fourth edition, thoroughly revised, of a laboratory guide for a course in elementary general zoölogy. It offers no particularly original features, but the material is well worked out pedagogically.

BOTANY

METHODS OF DESCRIPTIVE SYSTEMATIC BOTANY.

By A. S. Hitchcock. John Wiley and Sons

\$2.50 $6 \times 9\frac{1}{2}$; vii + 216 New York

In a thorough-going, practical way this book discusses the methodology of systematic botany. The beginner in any sort of taxonomic work has hitherto had to learn the technique of his trade by main strength and awkwardness, or by serving as an apprentice to some expert. With great skill and good judgment Doctor Hitchcock has produced a logical, well-ordered description of both the general principles and the details of this technique. There is no parallel treatise to this on the zoölogical side. Perhaps Doctor Hitchcock's successful achievement will stimulate some zoölogist to write one. In the meantime the beginning taxonomist in the animal world will find much that is helpful to him in this book.



THE AMERICAN OAKS. (*National Academy of Sciences Memoirs, Volume XX.*)

By William Trelease.

Government Printing Office

\$3.25 Washington, D. C.

$9\frac{1}{2} \times 11\frac{3}{4}$; v + 255; 420 plates

This is a thorough, detailed and comprehensive revision of the species of the genus *Quercus* found on the North Ameri-

can Continent. It is extensively and beautifully illustrated, and will stand for all time as a monumental piece of research in systematic botany.



A LABORATORY GUIDE FOR A COURSE IN GENERAL BOTANY.

By Lee Bonar, Richard M. Holman and Lucile Roush. John Wiley and Sons \$1.25 6 x 9½; xvi + 106 New York

This is an excellent laboratory outline for a college or university course in general botany, worked out at the University of California, and tested over a five-year period in mimeograph form before being reduced to print. The first part of the course gives the structure and functions of seed-bearing plants, carrying along physiological and morphological work side by side. The second part presents typical examples of the principle groups of plants for study, the work being made to bear directly upon the general principles of classification in the plant kingdom. Why is it that the pedagogy of elementary botany is so much better than that of elementary zoology, generally speaking?



BERGEY'S MANUAL OF DETERMINATIVE BACTERIOLOGY. A Key for the Identification of Organisms of the Class Schizomycetes.

By David H. Bergey.

The Williams & Wilkins Co. \$5.50 6½ x 9½; xvi + 462 Baltimore

This second edition of Bergey's well-known manual of condensed keys and species descriptions, for the determination of the taxonomic position of bacteria, differs from the first chiefly in alterations necessitated by changes in the nomenclatural status of genera, and in the addition of new genera and species described since the book was first issued. It is a

standard work in the field. There is an index of genera and species covering twenty odd pages.



GRUNDLINIEN ZUR ENTWICKLUNGSMECHANIK DER PFLANZENGEWEBE. (Abhandlungen zur theoretischen Biologie Heft 20.)

By H. Pfeffer. Gebrüder Borntraeger 6 Marks 6½ x 10; vi + 99 Leipzig

This volume presents a critical review of the literature on experimental morphology in the plant kingdom. While it is fair to say that, with a few exceptions, the botanical workers in this field seem to have drawn upon the school of Roux for their guiding ideas, the volume can be read with profit by the experimental animal morphologist.



MORPHOLOGY

A LABORATORY MANUAL OF THE ANATOMY OF THE RAT.

By Harrison R. Hunt. The Macmillan Co. \$1.25 5 x 7½; vii + 123 New York

The author suggests that the rat may well replace the cat or dog as a subject for dissection in college courses in vertebrate anatomy, and offers this manual as a laboratory guide for such use. By deliberate intent the book is not illustrated, which is probably a mistake from the standpoint of its specific pedagogical purpose, and certainly greatly reduces its value as a reference work. The whole treatment is rather elementary and superficial. What is needed is a treatise on the anatomy of the rat comparable in thoroughness and detail to Reighard and Jennings' *Anatomy of the Cat*.

DIRECTIONS FOR THE DISSECTION OF THE CAT.

By Robert Payne Bigelow.

The Macmillan Co.

\$0.90 5 x 7½; xi + 47 New York

This is a laboratory guide for the dissection of the cat, arranged to accompany Reighard and Jennings' long and favorably known treatise on the *Anatomy of the Cat*, to which specific page references are given throughout.



LABORATORY MANUAL OF THE FOETAL PIG.

By W. J. Baumgartner. *The Macmillan Co.*

\$0.90 5 x 7½; xii + 57 New York

Owing to the difficulty which the author alleges to exist in obtaining small mammals for material in courses in the comparative anatomy of the vertebrates, or for the mammalian portion of an elementary zoölogy course, the foetal pig is offered as a substitute, and the present volume as a laboratory guide for its dissection. Five general arguments are offered as to why the foetal pig is a good substitute. Three of these arguments seem very feeble indeed, and the fifth rather completely refutes whatever validity might have been supposed to inhere in the other four.



PHYSIOLOGY

ORALE REIZTHERAPIE. *Ein Beitrag zu der Stellungnahme Geheimrat Biers zur Homöopathie.*

By Arnold Zimmer. F. C. W. Vogel

5 Marks 6½ x 9½; 107 Leipzig

This book gives a detailed account of an extensive, experimental investigation carried out in the Surgical Clinic of the University of Berlin, undertaken for the purpose of scientifically testing the underlying tenets of homeopathy. The work seems to have been carefully done. The

results are somewhat surprising in indicating that perhaps there is more in the homeopathic theory than has commonly been supposed, particularly so far as concerns the size of dosage. The work has general biological interest to the student of *Reizphysiologie*.



REPRODUCTION IN THE RABBIT.

By John Hammond (with foreword and chapter on the formation of the corpus luteum by F. H. A. Marshall.) *Oliver and Boyd*

15 s. net 6 x 9; xxv + 210 London

This book constitutes No. IV of the useful series of Biological Monographs and Manuals of which the General Editors are Dr. F. A. E. Crew and Dr. D. Ward Cutler. It contains the account of a long experimental investigation, with an adequate review of the pertinent literature, on the physiology of reproduction in the rabbit. After a short introductory chapter on material and methods, the book deals successively with reproduction in the male; the female reproductive phases; the formation of the corpus luteum (contributed by Prof. F. H. A. Marshall, F. R. S.); ovulation and the Graafian follicle; the preliminaries to fertilisation; sterility; the effects of lactation; the duration of pregnancy; and a summary of the results. Brief but adequate bibliographies follow each chapter, and there are excellent author and subject indices. This is a book which every laboratory doing biological work of any sort with the rabbit as material, will need on its shelves.



MUSCULAR ACTIVITY.

By Archibald Vivian Hill.

The Williams & Wilkins Co.

\$2.75 5½ x 8½; 115 Baltimore

This volume contains the sixteenth course of lectures on the Herter Founda-

tion at the Johns Hopkins School of Medicine, delivered in 1924 by the Professor of Physiology in University College, London. They give a condensed account of Professor Hill's own important researches on the physiology of muscle in their relation to the general body of knowledge on that subject. Short bibliographies follow each chapter. The book is well indexed.



INFLUENCE OF THE THYROID GLAND ON OXIDATION IN THE ANIMAL ORGANISM.

By Edward C. Kendall

Columbia University Press

\$0.60 $6\frac{1}{2} \times 9\frac{1}{4}$; 36 (paper covers) New York

This is the lecture given on the occasion of the award to the author of the Charles F. Chandler Medal in Chemistry by the Trustees of Columbia University. It deals with the chemistry and physiological properties of thyroxin, the active principle of the thyroid gland obtained in crystalline form by Doctor Kendall.



LIGHT AND HEALTH. *A Discussion of Light and Other Radiations in Relation to Life and to Health.*

By M. Luckesb and A. J. Pacini.

The Williams & Wilkins Co.

\$5.00 $6\frac{1}{2} \times 9\frac{1}{4}$; viii + 302 Baltimore

Using "light" in an extended sense to mean "radiant energy" or "radiation," the authors have attempted to give a non-technical account of the present state of knowledge of the effect of light upon living organisms, and particularly man. After three general introductory chapters special chapters are devoted to the influence of light on the blood, the skin, the glands, the skeleton, the muscles, the nerves, the viscera, infectious diseases, hygiene in general, the senses, mental conditions, and health and happi-

ness in general. On some points the book is not at all critical of the evidence, but the most important defect is that throughout there is no indication of the sources from which the evidence is derived. Author's names are mentioned, but there is no slightest indication of where their writings are to be found, or what particular ones are referred to. This omission seriously reduces the value of the book for scientific purposes.



BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 178.* Containing following articles: *Verhütung von Laboratoriumsunfällen*, by Ferdinand Flury; *Indikatoren*, by E. E. Chapski; *Charakteristische Kohlenstoff-Stickstoff-Kondensationen der Carbonylkörper*, by Ernst Komm; *Acylieren*, by Fritz Wrede; *Die Veresterung der Carboxylgruppe*, by Franz Bachér.

Urban & Schwarzenberg

16,20 M. 7×10 ; 384 + xxiv Germany

Of the articles contained in this number of the Abderhalden Handbook of Biological Technique perhaps the first two are of the greatest interest to general biology. The first deals with the prevention of laboratory accidents, and the second with the chemical constitution, properties and uses of indicators. Both topics are discussed with genuine Teutonic thoroughness.



MIKROANALYSE NACH DER MIKRODENNSTEDT-METHODE.

By Casimir Funk. J. F. Bergmann

1,50 Marks $6 \times 8\frac{3}{4}$; 15 München

This little pamphlet deals with refinements of microchemical analysis. It is not entirely clear why it was thought necessary to publish these 15 pages as a book rather than as a contribution to some established chemical journal.

OXYDATION UND REDUKTION.

(*Handbuch der Biologischen Arbeitsmethoden, Lieferung 174.*)

By Richard Stoermer.

Urban & Schwarzenberg

21 Marks 7 x 10; 456 Berlin

This part of the Abderhalden Hand-book deals in great detail and completeness with the application of different oxydizing and reducing agents to the attainment of particular biological ends. It will be a useful reference work for the biochemist.



SEX

Vacant

(Because of the odd, but true, circumstance that no book falling in this field has reached THE QUARTERLY REVIEW OF BIOLOGY during the past three months.)



BIOMETRY

STATISTICAL METHODS FOR RESEARCH WORKERS.

By R. A. Fisher. Oliver and Boyd

15 shillings 6 x 9; ix 239 London
+ 6 pp. tables

This volume constitutes No. III of the series of biological Monographs and Manuals under the editorship of Doctors Crew and Cutler. It aims to give the biologist an account of the elementary biometrical technique useful in connection with the treatment of his problems. The viewpoint and methods of treatment are in some respects novel, representing the views of the author, who is one of the most distinguished of mathematical statisticians. While this is desirable and in every respect praiseworthy, it seems a little unfortunate that Mr. Fisher has

felt it necessary to use so extensively a new and somewhat confusing terminology. It is probable that on this account the biologist may find this book less useful practically than Yule's *Introduction to the Theory of Statistics*.



VARIATIONS IN THE COMPOSITION OF MILK.

By J. F. Tocher. H. M. Stationery Office
£1 1s. 7½ x 10½; 195 Edinburgh

This is a detailed and thorough biometric study of variation and correlation in the chemical composition of cow's milk. It is a substantial contribution to knowledge, and will stand as a valuable reference work. The author seems entirely unacquainted with the fact that any biometrical work has been done upon this subject in this country.



PSYCHOLOGY AND BEHAVIOR

WHY WE BEHAVE LIKE HUMAN BEINGS.

By George A. Dorsey. Harper and Brothers
\$3.50 5½ x 6½; xv + 512 New York

This non-fiction "best seller," by the one time Associate Professor of Anthropology in the University of Chicago and Curator of Anthropology at the Field Museum, attempts to tell in a volume which can be held in one hand the complete and up-to-date story of the raw materials of human nature and the possibilities of intelligent behavior. This is a large order, and, somewhat as in the case of Samuel Johnson's dog the wonder should be not that the author did not do a better job but that he attempted to do it at all. The whole range of general biology, anatomy, physiology, psychology, and anthropology, not to mention

medicine and hygiene, are called upon to furnish the elements for the account of why we are as we are, and behave as we do. While the turgid and clipped style in which the book is written will be offensive to some, and while others will not agree with the position taken by the author on certain questions, such as behavioristic psychology, it cannot be denied that Doctor Dorsey has produced an entertaining, popular scientific treatise on man. It will be found particularly useful by teachers of general biology for assignment as collateral reading. A brief bibliography and a thorough index complete the volume.



BEHAVIORISM.

By John B. Watson.

The People's Institute Publishing Co.

\$3.00 6 x 9; 248 New York

An extended review of this book is expected to appear in the next number of THE QUARTERLY REVIEW OF BIOLOGY.



INFLUENCING HUMAN BEHAVIOR.

By H. A. Overstreet.

The People's Institute Publishing Co.

\$3.00 6 x 8½; viii + 296 New York

We highly recommend this most entertaining volume to students of human and animal behavior. It concerns the technique of making people, individually or collectively, do what you want them to do. In particular this technique is developed relative to public speaking, advertising, and general writing. The book is well written and authoritative. The appalling thing about it is that it proves so conclusively the precision with which the technique works. Anybody who has any lingering doubts that there may possibly be such a thing as freedom of the will should read this book and see how simple

a matter it is for any skillful "go-getter" to make him do precisely what is wanted.

THE THYROID INFLUENCE ON THE BEHAVIOR OF THE WHITE RAT. (*Comparative Psychology Monograph, Vol. II, Serial No. 1.*)

By Edna Rickey.

The Williams & Wilkins Co.

\$1.50 6½ x 9½; 76 (paper cover) Baltimore

A detailed investigation indicated that either an excess or deficiency of thyroid gland substance unfavorably affected the behavior of the white rat. Especially in young animals an excess of thyroid gland substance induced hyperactivity and all learning or improvement in the skill and accuracy in behavior was practically impossible. The results obtained give some suggestion that the effects of alteration from the normal amount of thyroid substance in the body are transmitted to the offspring not themselves subjected to such alterations. Before accepting this conclusion, however, the geneticist will want further critical evidence.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

SINS OF SCIENCE.

By Scudder Klyce. *Marshall Jones Co.*

\$3.00 6 x 9½; 432 Boston

We shall allow this book to review itself. We believe that the extensive quotations given will not only entertain our readers, but will also sufficiently fulfil the stated purpose of this department of THE QUARTERLY REVIEW OF BIOLOGY to indicate "the character, the contents and the value of new books."

"So this book is unavoidably novel in several ways:

"(1) It states the answer to the bottom riddle of the universe—states what essential truth or religion really is.

"(2) It shows that the commonsense man practically knows the answer—and always has, since there have been men.

"(3) It shows that the real difficulty about essential truth is that the professional teachers of it, the so-called experts, have been tangled up in words. Hence the book, surprisingly, needs only to show what we common men already know practically:—how words work.

"(4) Because nearly all our leaders have held the riddle of the universe to be impossible of solution, I have become so interested in stating it clearly that I shan't be able (and won't try) to avoid displaying my interest hereafter. And such love of one's job is unfashionable, and hence novel, in this day of scientific detachment, disinterestedness, and cold-blooded neutrality or 'objectiveness.'

"(5) Finally, our intellectuals are teaching basic error, and (refusing to concern themselves with the whole truth) are leading trusting laymen, especially unprotected children, towards destruction. And I am strongly desirous of showing that error clearly, so that we can avoid its perverted teachers and protect our children" (p. 15).

"Indeed, science has never been able to see that the difference in its 'phenomena' is merely a *quantitative* difference of size of reversible components, and not any real difference—all phenomena being *essentially* the same. The reason scientists haven't been able to see that, is simply because they assumed, contrary to sound logic and observed facts and all commonsense, that one or more of the three components could be zero or infinity. In short, they confused One word with Many words.

"I.e., when they couldn't readily see or measure some small quantity, they dogmatically asserted it to be exactly zero—as we have seen repeatedly. Being materialists, they imagined that it was essential that they know such quantitative facts. So they weakly fooled themselves that they did. When they assert that the two transverse forces in gravity are exactly zero, obviously they materialistically assert that One words are Many words—and are wrong" (p. 255).

"You see, these biologists have got a basically wrong idea of importance and value. They are materialists, or consider *size* or *measures* as being *essential*. They in effect make a foot-rule their God, and worship it—which is idolatry, and plain stupidity.

"In short, it is rigorously proved that God or the universe, judged even by the *definite* requirements of the most materialistic biologists, is living, or a 'person.' The fact that all matter is personal, or alive in the sense of being conscious, is simply a truism of the existence of relationship, and has been seen throughout this book. But detailed proof of it will be given in the chapters on psychology" (*sic*) (p. 312-13).

"Thus it follows that representative leading scientists join with Millikan (as quoted above) in holding that I have not the remotest conception of what I am condemning in this book, have not made the slightest study of the evidence, that I act like a jungle beast, am like a dog, am a menace to democracy and civilization, lend myself as a responsible accomplice to moral and civic crookedness, am blind, prejudiced, unable to overcome a preconception, and intolerant. And I am in effect called all that, even though Millikan has advanced no proof or evidence that I am wrong. Quite to the contrary, he finally wrote me publicly (on March 7,

1924—the preface to his *Sc. and Life* is dated May 3, 1924), stating explicitly that he would agree with me that there can be no such thing as exact science” (pp. 321–22).

“So I should like to call attention to two facts about this book:

“(1) In every case where our common-sense views conflict with orthodox science, I have at least tried to give definite proof, *both logical and evidential*, of the correctness of our views. I may be badly mistaken in judging some of the *Many evidence*, and may even logically wobble on a few truisms. But at least I did try to give proof which any normal man could verify directly for himself, without relying on my assertions, or the assertions in any book.

“(2) And in no single instance do I attribute any wrong *motives* to scientists. I.e., I do not accuse any scientists of being somewhat deliberately crooked, or of being intentionally prejudiced, or of having the moral status of a dog or jungle inhabitant. (I sometimes quote their *own words* to that effect—but show that they probably exaggerate their own deficiency.) The sum total of my accusation against intellectuals is that most of them are ignorant, usually to the point of incompetency and often to the point of foolishness or borderline insanity, and that as a result their morals are often extremely bad from *our point of view*, but not intentionally so from *their point of view*. I undertake to *prove in considerable detail* that accusation I bring against them of ignorance. In no case do I accuse them of being voluntarily a menace—although they are dangerous to our welfare if we believe their false doctrines.

“Finally, the ‘worst’ specific action I recommend against them, is that we stop paying serious attention to them, warn our children against the danger of believing them, and stop paying their salaries and

endowments out of *our* pockets, *until* such time as *they* either stop teaching the materialism and agnosticism which we believe is false, or else convincingly *prove* to us that those doctrines are correct. They are of course at *liberty* to teach their dogmatic falsehoods if they wish—but *at their own expense*. They aristocratically or dualistically assume that because they are *superior* to us, therefore they are *privileged* to draw salaries from us to teach what *we* value at less than nothing. Any normal child who is a good American has better sense than to believe such divine-right-of-kings-or-professors (Chap. 17, §2).

“At present we do not believe their doctrines. Further, for nearly fifteen years I courteously and friendly submitted to them a definite and explicit disproof of those doctrines; and not once did they even *try* to rebut such proof. Invariably, those who don’t accept the proof act in one of these three ways: (1) they ignore the proof; (2) they call names, as Millikan has been quoted as doing; or (3) they say ‘Hush, Darling.’

That recommended specific action (of letting the scientists finance their errors), obviously is not intolerance on our part *in any Many sense*. It gives them ample opportunity to examine the evidence and correct their errors if they like. But if they do not wish to, or if they can’t (usually, they have badly spoiled their minds, and simply can’t), the extremest action against them is to protect our children from them, and stop paying them to propagate their error. When Millikan, in the typical scientific way, talks of such mild action as being wicked, he plainly shows that such action is needed.

“I submit Millikan and his colleagues’ own statement of their case and my statement of the case, to you, for you to judge. The intellectuals have repeatedly told me

in one way or another that I am unfair and am not sufficiently tolerant and patient. You can judge for yourself" (pp. 322-34).

The chief bibliographic source cited throughout the book is the *Encyclopaedia Britannica* (see). There is an index.



SCIENCE AND SCIENTISTS IN THE NINETEENTH CENTURY.

By Robert H. Murray. The Macmillan Co.
\$5.00 6 x 8½, xvii + 450 New York

This falls only a little short, in a few particulars, of being a great book. It is a realistic history of science in the nineteenth century, which proves, with the most elaborate documentation, that within that period substantially every important new discovery and important new idea in the realm of science met with the bitter and determined opposition of scientific men as a group. The leaders of this opposition always included many, if not the majority, of the most distinguished scientific men of the time. The author is a clergyman who is at the same time a trained historian. The motive underlying the writing of the book is to show that scientific men as a class are not a whit more open minded to new ideas than are theologians as a class. To the shame of scientific men it must reluctantly be admitted that Mr. Murray comes uncomfortably near to proving his case. Nor is this unfortunate situation improved by the specious argument of some apologists for science, who have discussed Mr. Murray's book, to the effect that critical skepticism is an integral part of science. It can be too easily shown that science has many times taken to its bosom the most arrant quackery without the slightest critical examination. In fact a strong case could be made that, in the whole intellectual history of mankind,

pseudo-science of all sorts has never flourished so extensively and respectably as it has in this twentieth century of grace. The most serious criticism of the book which can be made is that undue emphasis is given in some cases to relatively unimportant people and unimportant discoveries. The chapter headings are as follows: Jenner and Vaccination; Simpson and Chloroform; Lyell and Uniformitarianism; Helmholtz, Joule, and the Conservation of Energy; the Precursors of Darwin; Darwin and Evolution; Pasteur and Microbes; Lister and Antiseptics; Forgotten Scientists; Limitations of Scientists. There is a bibliography covering some 18 pages, and the book is well indexed.



MICROBE HUNTERS.

By Paul de Kruif. Harcourt, Brace and Co.
\$3.50 6 x 9; 363 New York

Objectively this is a history of the development of the science of bacteriology, in the form of biographical sketches of a dozen or so outstanding personalities in that development. But such a cold statement does not do justice to this book. For it is written *con amore*. On every page it is plain that the one passionate intellectual interest of Doctor de Kruif's life has been bacteriology. For him there are no heroes like its makers and no story so thrilling as theirs. A vast amount of painstaking research has obviously gone into the making of this book. The style in which it is written will offend the taste of many persons, as will also its naïve enthusiasms. Furthermore his probably sound estimate of Pasteur will bring down the wrath of those who in effect deify that great man. But in spite of all these considerations it remains the fact that the book is fascinatingly and thrillingly interesting.

Experimental tests show that he who begins at any point to read it is lost for the next two or three hours. And the guess may be hazarded that anyone who starts out to trip up Doctor de Kruif on his factual basis will find that he has essayed a tolerably difficult task.

ÜBER DIE LOGISCHEN PRINZIPIEN DER ÄRZTLICHEN DIAGNOSE. (*Abhandlungen zur theoretischen Biologie Heft 2.*)

By Fritz Mainzer. Gebrüder Borntraeger
3 Marks 6½ x 10; iii + 51 Leipzig

The problem with which this volume has to do offers many entertaining pos-

sibilities, but unfortunately the treatment of it here falls a bit on the ponderous, not to say dull, side. The book is an attempt at a philosophical examination of the underlying principles of clinical diagnosis. It examines, in considerable detail, the logical foundations of actual present practice in diagnosis, points out logical weaknesses in the procedure, and suggests logical improvements. There is considerable discussion of the theory of probability in relation to clinical diagnosis. Somewhat unfortunately, there is no attempt at a systematic review of the literature which has dealt with the underlying philosophy of clinical work.



THE QUARTERLY REVIEW of BIOLOGY



ABNORMAL SEXUALITY IN ANIMALS I. GENOTYPICAL

By F. A. E. CREW

Animal Breeding Research Department, University of Edinburgh

IN A review of a field of biological enquiry in which great activity prevails, it is inevitable that much that is ill-understood, debated, disputed, shall be treated in a somewhat arbitrary and even dogmatic manner. It is inevitable too that the reviewer must be found guilty of the faults of misunderstanding, of misinterpretation, and of misused emphasis. Much of great suggestiveness has been omitted since the exigencies of space have made it necessary to prefer just that material which should make the story march easily.

The space at the disposal of the writer does not allow a complete review. The present contribution is therefore limited to the genetics of the subject; the physiological aspects of abnormal sexuality in animals will be reviewed in an early number of the *QUARTERLY REVIEW OF BIOLOGY*.

SEXUALITY

Sex is the term used to define that differentiation of different parts of an individual, or of the individual itself at different times, or of different individuals,

which is associated with the elaboration of physiologically and often morphologically dissimilar gametes. Maleness is the state or quality associated with the elaboration of spermatozoa (or of their physiological equivalents); femaleness is the state or quality associated with the elaboration of ova (or of their physiological equivalents). Sexuality is the state or quality of being distinguished by sex. A male is an individual that exhibits the state or quality of maleness; a female one that exhibits the state or quality of femaleness. If in a group (e.g., a species) it is customary for maleness and femaleness to be exhibited by one and the same individual, coincidently or in succession, the group and the individuals comprising it are monoecious, hermaphrodite, though it follows that in certain cases an individual can at one time be a male and at another a female. If in a group it is not customary for maleness and femaleness to characterize one and the same individual, the group is dioecious, bisexual; the sexes are separate, and every individual within the group throughout its sexual life is either a male or else a female.

Though attempts to classify the sex-dimorphic characters for purposes of discussion have been many, it has to be confessed that as yet no satisfactory classification exists. That this is so is due to the fact that as yet no exact knowledge exists concerning the genetic nature of many of these characters and of their relation to the sex-glands, and until this has been secured any attempt to classify them must be premature. For the present it is enough to hold that the characters which in their combination constitute maleness and femaleness respectively are characters

environment, established by the whole of the genotype in action and by the functional activity of the characters as these become differentiated. As a working hypothesis, it can be accepted that sexuality is primarily based upon antecedent determiners within the germ-plasm, upon genes resident in the chromosomes.

In an ever increasing number of instances it can be shown that the phenotypic differences distinguishing male and female are associated with constant differences in the chromosome content of the tissues of the two sexes. This fact is illustrated

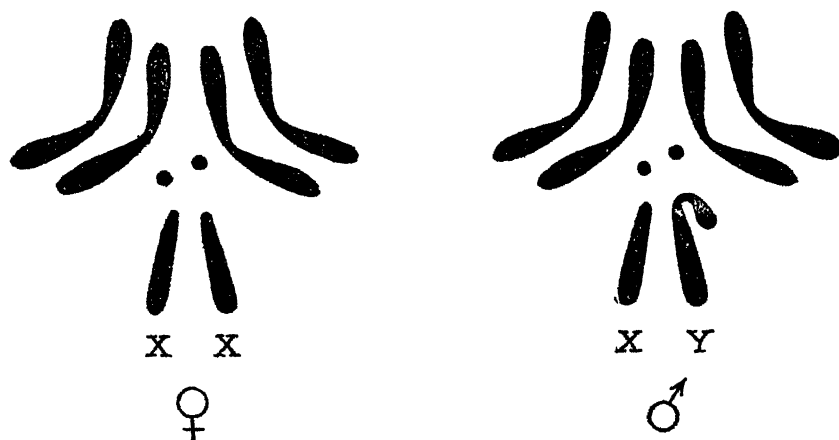


FIG. 1. CONVENTIONAL DIAGRAM OF THE CHROMOSOMES OF *Drosophila melanogaster* (AFTER MORGAN)

in the genetic sense, being expressions of a genotype that is determined by the nature of the genes brought into the zygote by the conjugating gametes. In the fertilized egg there are none of the characters that distinguish race from race, male from female, that make each individual the first and last of its identical kind; these are expressed as ontogeny proceeds and their expression is modelled, encouraged, embarrassed, to a greater or lesser extent, by the impress of the agencies of the external environment, the outer world, and by the changing conditions within the developing zygote itself, the internal en-

vironment, established in the clearest possible manner in the case of *Drosophila melanogaster* which has four pairs of homologous chromosomes. In the somatic cells and immature gametes of the male one of the four pairs is remarkable in that its members are morphologically dissimilar whereas in these tissues of the female the members of this pair are, as is the case in all the other pairs in both male and female, morphologically alike. Since tissues from male and female differ chromosomally only in this respect, these chromosomes are referred to as the sex-chromosomes and the members of the sex-chromosome pair in the female and the

one sex-chromosome of the male that is morphologically similar to these are known as the X-chromosomes, whilst the unequal mate of the X in the male is known as the Y-chromosome. In respect of the sex-chromosomes the female is XX, the male is XY.

The situation thus arises that in all the cells of the body of the female and in her immature ova there are four pairs of homologous chromosomes, and of these one pair consists of two X-chromosomes, whereas in all the somatic cells and immature gametes of the male there are four pairs and of these one consists of an X-chromosome in association with a Y-chromosome. Into each ripe gamete there passes one or other member of each pair. All eggs are alike in that each contains an X-chromosome but there will be two kinds of sperm, one containing three autosomes and one X-chromosome, the other three autosomes and a Y-chromosome. When egg and sperm unite in fertilization, into the zygote will be received one member of each pair from the father by way of the sperm and the other member of each pair from the mother by way of the egg, and there will be two forms of zygotes, one that received an X-chromosome by way of the sperm, the other that received a Y-chromosome. The first will have a sex-chromosome constitution that can be symbolized as XX, the chromosome constitution typical of a female, the other a sex-chromosome constitution symbolized as XY, that of a male.

In other cases the chromosome difference between the sexes takes the form of a difference in the number of the sex-chromosomes; for example, there may be in one sex a single X-chromosome, as in the male of many mammals, while in the other there are two. In other groups, e.g., the bee, male differs from female in that one sex is haploid in respect of its

chromosome number, possessing but half the number characteristic of the opposite (diploid) sex. It will be seen, as the argument proceeds, that there is considerable difficulty in bringing this type of chromosome difference into line with others, and one is tempted to wonder if all the facts concerning the relation of sex and chromosomes in this group are known.

Our knowledge of the genetics of *Drosophila*, based upon the magnificent and

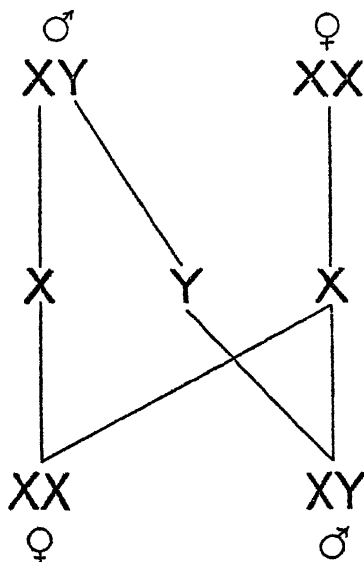


FIG. 2. THE SEX-CHROMOSOME SEX-DETERMINING MECHANISM

inspiring work of Morgan and his associates, is such as to warrant the statements that hereditary characters are the end-results of the action of genes resident in the chromosomes; that in one and the same chromosome is resident a certain orderly company of genes; that each gene has its own particular locus in a particular chromosome; that the genes are arranged in a definite linear order in the chromosome; and that a gene is a certain local area of active chromatin exhibiting a definite

kind of organization capable of undergoing reorganization spontaneously, or maybe under the impress of certain as yet undefined environic stresses, and that it exerts its action and produces its end-results through the medium of the products of its metabolism, substances possibly enzymatic in nature.

The facts of sex-linkage (Morgan, 1914) non-disjunction (Bridges, 1916), and deficiency (Bridges, 1917; Mohr, 1923) are sufficient to warrant the assertion that in *Drosophila* the Y-chromosome is physiologically inert, containing no genes. It follows then that in the case of the female tissues there are two X-chromosomes in association with two of each of the autosomes, so that if A represents one complete set of autosomes as present in the ripe egg, the quantitative relation, in the body cells of the female, in the gametes, and in the XX type of zygote, between the chromatin in the sex-chromosome and that in the autosomes can be expressed by the formula $1X:1A$, whereas in the male somatic cells and immature gametes and in the XY type of zygote it is expressed by the formula $1X:2A$. In the X-chromosome bearing sperm the relation is $1X:1A$, in the Y-bearing $0X:1A$. The fact that the egg and one kind of sperm are both, in this respect, $1X:1A$ and that the other kind of sperm is $0X:1A$ is of interest in that it shows quite conclusively that gamete and zygote are entirely dissimilar in spite of the fact that each may exhibit a similar X:A ratio. In non-disjunction it is common to get an XY-bearing egg which is, in every way, an egg and in no way is an XY individual, a male. That part of the genotype which is concerned in the morphological aspects of sexuality in the zygote is not liberated until egg has been activated by sperm. As will be seen, the genotype of the gamete has no constant relation to the structure

of the gamete for the latter is determined by the kind of organization of the gonad that manufactured it: an ovary elaborates eggs without reference to their genotype and a testis elaborates sperm without reference to their genotype. A gamete $1X:1A$ in genotype will be an egg if it is the elaborated product of an ovary: a sperm if it is elaborated by a testis.

Since it is established that the genes in the X-chromosomes are different, as judged by the end-results of their action, from those on the autosomes, and that the chromatin organization of any chromosome can exhibit change, it follows that chromatin of the X and of the autosomes is different in its organization and therefore in its physiological activity. Thus the quantitative balance between the X-borne and the autosomal-borne genes differs in male and female tissues and the physiological states established by the interaction of genes in male and female zygotes respectively will likewise be dissimilar.

It is not necessary, it is probably entirely incorrect, though it is undoubtedly convenient, to postulate male-determining and female-determining genes, especially concerned in determining sexuality. Maleness in *Drosophila* is that physiological state or quality established in a zygote as the result of the action and interaction of all the genes in a genotype that may be symbolized as $1X:2A$. In the beginning, maleness in the zygote is a certain kind of internal environment, a certain metabolic level: femaleness is another, and in one or the other organogeny and ontogeny proceed. In the XX type of individual an internal environment of femaleness becomes expressed and the structures that pertain to the sexual organization will pursue their differentiation under the direction of their own genotype, in the presence of the physiological stimuli exerted by other differentiating and dif-

ferentiated tissues, and in an external environment which may condition this differentiation. On the other hand, in the XY zygote an initial internal environment of maleness becomes established and the differentiation of the sexual organization during ontogeny will be such as will yield a typical phenotypic male.

An individual in the case of *Drosophila* is a phenotypic male (1) because in the beginning it was a genotypic male (XY); (2) because in this XY zygote the relation between the X-borne and the autosomal-borne genes (the ratio between their number or their algebraic sum, as suggested by Schrader and Sturtevant (1923) as an explanation of the facts of sexuality in those cases in which one sex is haploid, the other diploid) was such that an internal environment of maleness became established; (3) because in this internal environment the structures concerned in the sexual organization, being XY in chromosome constitution, developed, and in developing flourished; and (4) because the impress of the external environment did not or could not affect the developing zygote in such a way as to override the effects of the gene mechanism and to modify the internal environment based thereupon so that it became physiologically equivalent to that type of internal environment that is normally associated with the genotype symbolized as XX. For similar reasons the genotypic female becomes a phenotypic female. *Propter secretiones internas totas mulier est quod est*, a female is a female by the totality of her internal secretions, remains true only if it be granted that the phrase "internal" secretions shall include the metabolic products of her initial genotype.

In the vertebrates the initial sexuality, which is but the direct expression of genetic action, is strongly reinforced when the components of the endocrine system

become differentiated. The results of experimental gonadectomy and of the implantation of gonadic tissues have clearly demonstrated the intimate relation between the type and degree of sexual differentiation and the functional activity and histological organization of the gonads (Steinach, 1912; Sand, 1921, 1923; Moore, 1921; Lipschutz, 1924). They have shown conclusively that for the complete differentiation and maintenance of the sexual phenotype active functional gonadic tissue is essential, that a male possessing testes, because the embryonic gonads assumed the testicular organization for the reason that they were XY tissues and developed in the initial internal environment of maleness, becomes a phenotypic male because the testes exhibited a certain specific kind of physiological activity, elaborated a specific male "sex-hormone" which greatly reinforced the initial internal environment of maleness and exerted, during the critical period of their development, a directing stimulus that evoked a ready response on the part of the remaining structures of the sex-equipment so that these pursued their differentiation according to the male type of sexual architecture. They have shown that an individual becomes a phenotypic female because it possessed functionally active ovaries at the time when the rest of the structures of the sex-equipment underwent differentiation. When it has been shown how it is that she comes to possess ovaries, there remains no difficulty in showing how it is that she becomes equipped as an efficiently functional female.

It is not to be denied that for the efficient differentiation and maintenance of the sexual equipment the activity of other members of the endocrine chain is essential (Bullock and Sequira, 1905; Glynn, 1911-12; Berner, 1923; *et alia*), but for the pres-

ent it is reasonable to assume that the rôle of such glands as the adrenal, the pituitary, the thyroid, in sexual differentiation, is relatively unimportant when compared to that of the differentiated gonad.

Reviewing that which has been written above, the sexual characterization in the

(Painter, 1921-1924; Bachuber, 1916; Stevens, 1911; Wodsdalek, 1913, 1914, 1916, 1920; Winiwarter and Sainmont; 1909; Allen, 1918; Malone, 1918; Zeleny and Faust, 1915; Parkes, 1923; Yocum, 1915, 1917). (See table 1.)

Reasons for holding that the gonads, in

TABLE 1

	MALE	FEMALE
1. <i>Primary genotypic sexual characters</i>		
<i>The sexual genotype</i> symbolized as	XO or XY	XX
in action establishes		
<i>an internal environment</i> symbolized as	1X:2A	1X:1A
in which ontogeny proceeds and the phenotype is assumed		
<i>Secondary genotypic sexual characters</i> are developed.	Such sexual differences as are not secondary gonadic (many of them are epigamic, i.e., concerned only indirectly with, but contributory to, fertilization, playing their part in courtship and the care of the young)	
These include:		
2. <i>Primary gonadic characters</i>		
The gonads become differentiated	Testes	Ovaries
The 'sex-hormone' is liberated and the following become differentiated	Male sex-hormone	Female sex-hormone
<i>Secondary gonadic characters</i>		
(1) The accessory sexual apparatus (Müllerian and Wolffian ducts)	Wolffian duct derivatives flourish Müllerian duct derivatives cease their development	Müllerian duct derivatives flourish. Wolffian duct derivatives cease their development.
(2) The external genitalia	Scrotum	Vulva
Urogenital sinus	Penis	Clitoris
Phallus		
(3) Certain of the epigamic characters which for their expression depend upon the stimulus of the differentiated gonad, and becoming expressed at different times as they reach the stage of their development when they can respond	e.g., regional distribution of hair, mammary glands, voice.	

mammal can be summarized, for purposes of discussion, as follows. It is to be noted that in the case of the bird the female is the digametic sex (XY) and the male monogametic (XX). In the vertebrate groups that have been examined the sex-chromosome constitution is as that which obtains in the case of *Drosophila*.

certain vertebrate groups, e.g., birds, do not function as endocrine glands, elaborating specific sex hormones, will be considered later.

In the case of insects (Oudemans, 1899; Kellogg, 1904; Prell, 1915; Kopeć, 1911, 1922; Meisenheimer, 1909; Hegner, 1914) it has been established by experimental

gonadectomy and the implantation of gonadic tissues that no part of the control of sexual differentiation is, in these forms, relegated to the gonad. All the sexual characters of the insect are secondary genotypic and owe nothing in their differentiation to the physiological activity of the differentiated gonad. The differentiation of a cell is pursued under the control of its own genotype.

Finkler (1923) has carried out some vastly interesting experiments with various orthoptera (*Hydrophilus*, *Dysticus*, *Notonecta*, *Dixippus*, *Tenebrio*, *Vanessa*). He transplanted male heads on to female bodies and *vice versa* and observed the effect of this upon sexual behaviour. In the case of *Hydrophilus*, three operations were entirely successful, complete healing occurring in about seventeen days when all movements were properly coordinated, and feeding and defecation were normal. A female with a male head behaved sexually as a male towards females and a male with a female head as a female, but was regarded by normal males as a male. In certain instances the body took on the coloration of the sex to which the transplanted head belonged. Blunck and Speyer (1924), repeating this work, failed to confirm Finkler's findings.

ABNORMAL SEXUALITY

1. INTERSEXUALITY

If in an individual of a group in which bisexuality is customary, maleness and femaleness are exhibited coincidentally or in succession and to any degree, that individual is an intersexual form. It is an intersex either in time or in space. Intersexuality is the state or quality exhibited by an individual of a normally dioecious group in which both maleness and femaleness are to be distinguished in varying degree and/or at different times. Her-

maphroditism is the expression of a sexuality normal to a particular group: intersexuality, transient or permanent, an expression of sexual abnormality in a particular group or individual. Hermaphroditism and intersexuality are the same expression of the self-same mechanism but whereas intersexuality is perfect or imperfect hermaphroditism in a non-hermaphroditic group or individual, hermaphroditism is perfect intersexuality in a group or individual in which such a state or quality is a customary feature of the normal life history.

From what is known of the mechanisms of sex-determination and sexual differentiation it can be anticipated that intersexuality in a normally dioecious group will follow upon (1) disharmony in the sexual genotype of the body as a whole or of local parts, and (2) profound alteration of the internal environment during critical stages of development.

A. Disharmony in the distribution of the genotype

1. *Gynandromorphism.* (a) *Gynandromorphism in Drosophila melanogaster.* A gynandromorph is an individual of a bisexual species which exhibits a mosaic of male and female sexual characters: it is a sex mosaic in space. In the case of *Drosophila melanogaster* about 1 in every 2,000 individuals exhibits this condition of gynandromorphism. Most of these are bilateral gynandromorphs, exhibiting the complete male characterization on one side of the antero-posterior mid-line of the body, the complete female characterization on the other, with a sharply demarcated line of junction of the two kinds of tissue. Since the male body is normally smaller than that of the female the gynandromorph's body is bent towards the male half. Usually in these cases there is an ovary on the female side, a

testis on the male, but this is not always the case, nor would it be expected that it should be, for, as Huettner (1922) has shown, the gonads are not formed from a single nucleus but from several nuclei which give rise to the primordial germ cells and so it is not inevitable that both gonads should be histologically and cytologically similar. Commonly, however,

forms in great detail and have shown that if in the mating that produces the gynandromorphic forms sex-linked characters are involved, and if the sex-linked characterizations of the two parents are dissimilar, then the sex-linked characters of the male parts are those exhibited by the father or those exhibited by the mother whereas the sex-linked character

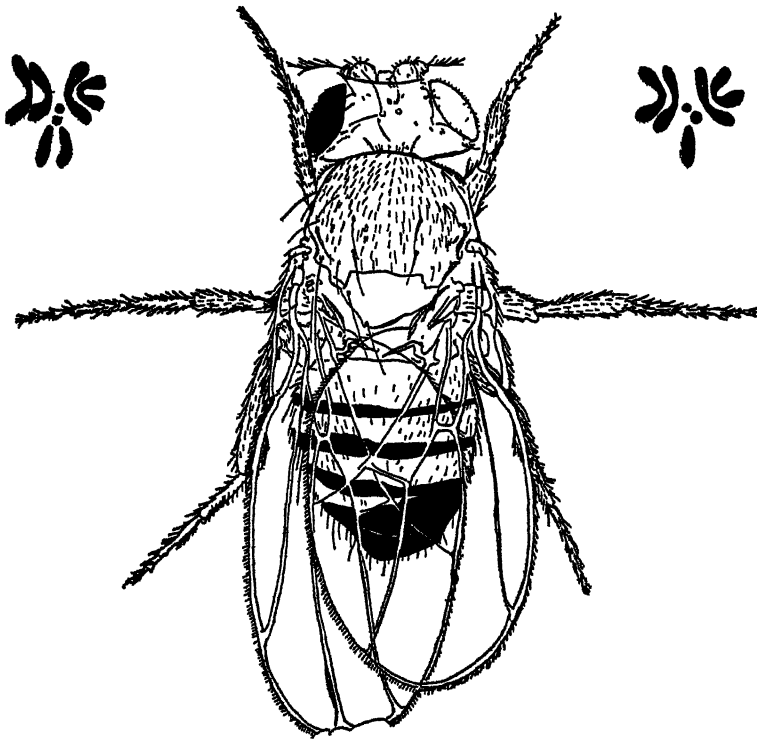


FIG. 3. A GYNANDROMORPH (FROM MORGAN, BRIDGES AND STURTEVANT)

they are two ovaries or two testes in a bilateral gynandromorph. In other cases of gynandromorphism one quarter of the body is male in its sexual characterization, three quarters female: in still others less than a quarter is male and more rarely the head is female whilst the rest of the body and abdomen are male.

Morgan and Bridges (1919) have described many of these sexually abnormal

of the female parts are a combination of the sex-linked characters of both parents, and that, in respect of the autosomal (non sex-linked) characters, male and female parts are alike. The example depicted above is a bilateral gynandromorph, the left side exhibiting a typical female characterization, the right a typical male. The left side presents the dominant sex-linked character, Notch, (the mother was

Notch), and the right exhibits the recessive sex-linked characters scute, broad-wing, echinus eye, ruby eye, tan body-color, and forked bristles (the father had these characters).

These facts point to the conclusion that gynandromorphism in such a case as this results from aberration in the distribution of the X-chromosomes. If it is assumed that the gynandromorph is in its beginning an XX-zygote, a genotypic female, and that at some stage during the early cleavage divisions of the fertilized egg, a daughter X-chromosome fails to enter one of the daughter cells, this cell will then contain one X instead of two, i.e., will have the chromosome content of a genotypic male. Since one X is derived from the paternal contribution of nuclear material and the other from the maternal and since, if the parents were dissimilar in their sex-linked characterization these two X-chromosomes will be dissimilar in their gene content, it follows that the characterization based upon genes in either of them can be markedly different from that based upon the genes in both. In the example described above the mother (XX) carries in each of her X-chromosomes (shaded) the gene for the dominant sex-linked mutant character Notch. The father (XY) carries in his single X-chromosome (unshaded) the genes for the recessive sex-linked characters scute, broad, echinus, ruby, tan, and forked. The F_1 female zygote will receive one X-chromosome from each parent. She will exhibit the dominant character Notch and not scute, not broad, not echinus, not ruby, not tan, and not forked—the dominants of both parents. If during the first cleavage division of this zygote the maternal X-chromosome fails to enter a daughter cell the paternal X alone will be present therein and the tissues that develop from this daughter cell will be 1X:2A (male)

in constitution and cannot be Notch but will exhibit, if they belong to the appropriate parts, the recessive sex-linked characters of the father. Had it been the paternal X that had been eliminated, the male side of the gynandromorph would have exhibited the sex-linked character of the mother, Notch.

In the absence of further aberrations in chromosome distribution all the cells that have their origin in the XX daughter cell will have the 1X:1A type of chromosome relationship: all the cells that arise from the single X-containing daughter cell will have the 1X:2A type, and the sex-linked characters of the tissues formed by these latter will exhibit, if they pertain to parts that do exhibit sex-linked characters, those of the parent from whom their X-chromosome was derived. If this is the case, then a gynandromorph of a grade that is compatible with fertility, i.e., one in which the abdomen and genitalia are female, should prove to be heterozygous in respect of her sex-linked characterization. This is the case. On the other hand, if the abdomen and genitalia are of the male type of architecture, the individual should be sterile, since in these parts the sex-chromosome constitution is XO and it is known from Bridge's non-disjunctional work (1916, 1919) that the XO male in *Drosophila* is sterile. This is also the case.

If the elimination of the X-chromosome occurs at the first cleavage division of the zygote, the gynandromorphism is bilateral: if it occurs at the second, one quarter of the body will be male in its characterization. Elimination may occur at any stage of ontogeny and the later it occurs the smaller will be the area that exhibits male type characterization. But however large or small this area may be, it will pursue its development under the direction of its own genotypic constitution

(except in the case of vermillion eye, Sturtevant, 1920) and its differentiation is not influenced by the physiological activity of the gonads.

It is to be noted that these mosaic formations are not limited to the sexual phenotype: they are commonly found involving the general phenotype in hybrids.

tion of an X-chromosome at a cleavage division, but one specimen was a mosaic both for sexual characters and for mutant characters in chromosome III. Analysis of this case showed that in its production two spermatozoa were involved and that it was the result either of the synchronous fertilization of a double nucleus egg by

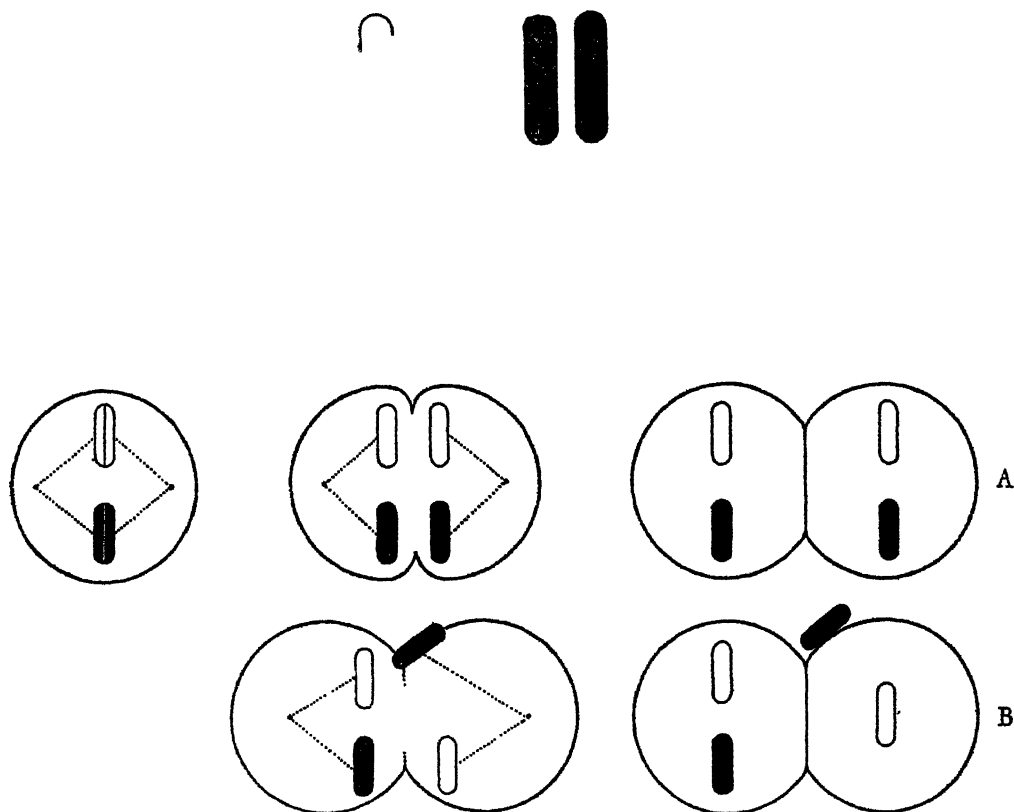


FIG. 4. GYNANDROMORPHISM FOLLOWING THE ELIMINATION OF AN X-CHROMOSOME
A, normal distribution of chromosomes; B, abnormal distribution of chromosomes

Gynandromorphism results only from such aberrances in the distribution of nuclear chromatin that lead to a sufficient disturbance in the X:A ratio.

(b) *Gynandromorphism in D. simulans*. Gynandromorphs have occurred fairly commonly in *Drosophila simulans* (Sturtevant, 1921). Most of these are to be interpreted as the result of the elimina-

tion of two sperm or to polyspermy in a single nucleus egg.

(c) *Gynandromorphism in the bee*. There are certain facts relating to sex-determination in the bee that are unique. The queen is diploid and this double set of chromosomes is reduced to the haploid number in the ripe egg after two polar bodies have been extruded. If the egg is

fertilized, it gives rise to a female (queen or worker) but if it is not fertilized it yields a male (drone). The male has the haploid number of chromosomes but whether sex-determination is the result of the action of a chromosome mechanism has not yet been determined. It is necessary to assume that the sex-determining mechanism in the bee and similar forms is essentially different from that which obtains in the case of *Drosophila*. It is remarkable that the male is a haploid individual and that the diploid individual is not a male for the ratios among the sex-determining genes are not different in the two cases. The case of the bee is so unique that it merits further investigation. Disagreement with a system that obtains so widely, and an interpretation that is so satisfactory must always be a stimulus for further investigation and not merely a missile for a critic's hand.

In the bee the mother transmits her characters directly to her sons as is the case in the typical sex-linked mode of inheritance in *Drosophila*. But the reason for this is that the male develops from an egg that has received no paternal chromatin. There is certain reliable evidence which strongly suggests that there is a chromosome in the bee that is equivalent to the X-chromosome of *Drosophila*. Hybrid queens produce two kinds of males and two only, which fact indicates that a single factorial difference exists and that the allelomorphs are carried by a pair of chromosomes, not necessarily sex chromosomes, but possibly so. The elimination hypothesis which seeks to explain gynandromorphism in the bee demands that the elimination must involve a sex-chromosome and that this must also be the one that carries the genes concerned in the production of racial characters.

In the sixties of the nineteenth century Eugster kept at Constance a hive of bees

which consisted of hybrids out of a yellow Italian queen by darker German drones and which regularly produced a large number of gynandromorphs. This regularity in the production of abnormal forms points to the conclusion that the abnormality is genetic and not merely accidental or due to specific environmental impresses. When the Italian queen died Eugster replaced her with a hybrid queen and she in turn produced gynandromorphs. V. Siebold first examined these specimens in 1864, and attempted to account for these gynandromorphs by assuming that an insufficient number of sperm had penetrated the egg so that parts of it lacked sufficient quantities of the male contribution. It is to be noted that Nachtsheim (1913) has since shown that polyspermy is customary, but this interpretation does not explain all the phenomena encountered. They have been re-examined by Boveri (1915) and Mehling (1915). The specimens ranged from an almost perfect male to an almost perfect female. Since they were hybrids, it was possible to tell from their characterizations whether the tissues concerned contained paternal, maternal, or both paternal and maternal nuclear material. Boveri concluded that all the male parts were purely Italian in their characterization, whereas the female parts were definitely hybrid, exhibiting the characters of both races. If this were so, it follows that in the tissues of the male parts there was no nuclear material brought into the zygote by the sperm but only that contributed by the ovum.

In order to explain this, Boveri suggested that the sperm did not reach the egg nucleus before the latter had begun to segment and so fused, not with the whole egg nucleus, but with one of the daughter nuclei (partial fertilization). Two blastomeres would thus result, one containing

only the maternal nucleus whilst the other would include both maternal and paternal nuclear material. It is established that in the case of the bee, if the egg which contains the haploid number of chromosomes is fertilized it becomes a female: if it is not fertilized, it becomes a male. The male is haploid, the female diploid in respect of its chromosome content. It follows then, that in the case of the late fertilized egg, the blastomere that contains both maternal and paternal nuclear material is diploid, i.e., female, the blasto-

mother's race (Italian) because its haploid chromosomes came directly from the Italian mother egg, whilst the female side should exhibit the dominant characters of both Italian and German races. If, on the other hand, the condition results from polyspermy, then the male parts should exhibit the characters of the father's race (German). Boveri, examining the preserved specimens (47 years in alcohol), reached the conclusion that the male parts were Italian in their characterization. If this is the case, then Boveri's hypothesis is to be preferred to that of Morgan.

But Engelhardt (1914) has described some fresh gynandromorphic specimens out of an Italian mother by a father very similar indeed to that of the males of the Eugster hive. The male parts presented the paternal characterization. This supports Morgan's interpretation.

Morgan and Bridges are of the opinion that the case of Eugster's bees can equally readily be explained by assuming that, as in the case of the *Drosophila* gynandromorphs, there is an accidental elimination of a sex-chromosome during cleavage. The bees concerned were *A. ligustica* (Italian), and *A. mellifica* (German). If it is assumed that one of the postulated sex-chromosomes of the hybrid carried the gene-complex for the *ligustica* characterization, the other the *mellifica*, and if the *mellifica* chromosome is eliminated, then a cell containing only the *ligustica* chromosome would result and all parts descending from that cell would be male (haploid) and *ligustica*. This is the result observed by Boveri. If the *ligustica* chromosome is eliminated the result is male tissue and *mellifica* characterization. This is the result observed by Engelhardt. This interpretation accommodates both Boveri's and Engelhardt's observations whereas Boveri's partial fertilization and

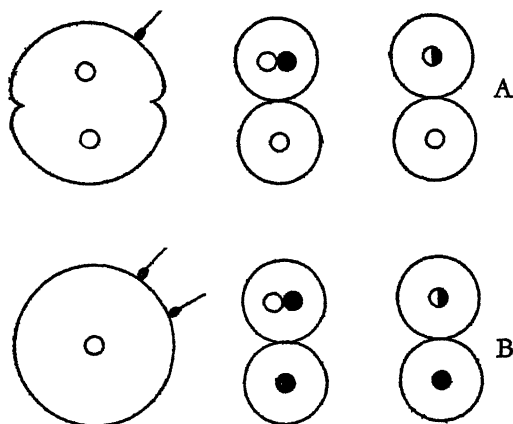


FIG. 5. INTERPRETATIONS OF GYNANDROMORPHISM

A, partial fertilization of Boveri, B, polyspermy of Morgan.

mere that is not fertilized remains haploid, i.e., male.

Morgan has suggested that the same results would follow if two sperms should enter one and the same egg, but only one of them unite with the egg nucleus (polyspermy). Doncaster (1914) has pointed out that, as seen in his *Abraxas* work, this gynandromorphism could be explained as the result of the synchronous fertilization of two egg nuclei.

If the gynandromorphism is the result of partial fertilization, then the male side should exhibit the characters of the

Morgan's polyspermy each only explains one. If *melifica* is dominant to *ligustica*, then the female parts will be *melifica* as described by Boveri. But Newell (1914) who crossed Italian queen and gray Carniolan drone got yellow daughters, showing that the yellow was dominant. In this case both sides would be alike if in the male parts the *melifica* chromosome had been eliminated, and this may have been the reason for v. Siebold's omission to mention in connection with the fresh Eugster specimens that the parts were

which the chromosome distribution is abnormal, the end-result will be bilateral, quartal, or some other grade of sex mosaic.

For further instances in other forms see Sandhouse (1923), Wheeler (1910), and Nachtsheim (1923).

(d) *Gynandromorphism in the silkworm*. Among the Lepidoptera over 1,000 cases have been described (see Wenke, 1906). They can all be explained on the assumption that there has been elimination of an X-chromosome in the XX (male) zygote. Toyama (1906) has described

$\frac{\text{Egg}}{(\text{WX})}$	\times	$\frac{\text{Sperm}}{(\text{wX})}$	This half will develop, will be male (XX) and zebra (Ww)
$\frac{(\text{WX})}{\text{Y}}$	\times	$\frac{(\text{wX})}{\text{Y}}$	This half will develop, will be female and zebra.
$\frac{\text{Y}}{\text{Y}}$	\times	$\frac{(\text{wX})}{\text{Y}}$	This half will develop, will be female and white
$\frac{\text{Y}}{\text{Y}}$	\times	$\frac{\text{Y}}{\text{Y}}$	This half will not develop.
<i>Morgan's polyspermy interpretation.</i>			
$\frac{(\text{WX})}{-}$	\times	$\frac{(\text{wX})}{-}$	This half will develop, will be male and zebra.
$\frac{(\text{WX})}{-}$	\times	$\frac{(\text{wX})}{-}$	This half will develop, will be female and white.
$\frac{\text{Y}}{-}$	\times	$\frac{(\text{wX})}{-}$	This half will develop, will be female and white.
$\frac{\text{Y}}{-}$	\times	$\frac{(\text{wX})}{-}$	This half will develop, will be female and white.
<i>Morgan's elimination interpretation.</i>			
(WX)	(wX)		The zygote.
(WX)	(wX)		This cell and the tissues arising therefrom will be male and zebra.
$\frac{(\text{WX})}{\text{or } (\text{wX})}$			This cell and the tissues arising therefrom will be female and zebra if one X is eliminated, white if the other.
$(\text{WX})\text{Y}$			The zygote
$(\text{WX})\text{Y}$			This cell and the tissues arising therefrom will be female and zebra.
Y			This cell will not develop.

different in colour. It is not improbable that when Boveri examined his material the specimens were too old to give reliable pictures of color differences. Whichever interpretation is correct, and there is no reason to assume that all instances of gynandromorphism result from exactly the same kind of fault, it is certain that in all cases the underlying cause of gynandromorphism is an abnormal distribution of nuclear material; it is the mechanism of distribution that is at fault. According to the stages of embryonic development at

two cases in the silkworm moth (*Bombyx mori*). The mother belonged to a race in which the caterpillar is zebra patterned and the father was of a race in which the caterpillar is uncolored white. Zebra is dominant to white, and these characters were regarded as being sex-linked. In the one case the left female side was zebra, the right male was white.

Boveri's partial fertilization interpretation. The female is XY in the silkworm. She lays two sorts of eggs, the X-bearing and the Y-bearing. Either of these is fer-

tilized by an X-bearing sperm. Let W = the gene for the zebra pattern, w that for white, and let the brackets represent the fact that the gene is resident upon the X-chromosome included therein.

None of these interpretations accommodate the facts of the case. Fortunately Doncaster (1914) had described binucleated eggs in *Abraxas*, each nucleus having given off polar bodies and each having been independently fertilized. Morgan, appealing to this fact, points out that if the zebra mother was heterozygous for this character one nucleus could contain an X-chromosome and an autosome with the gene for white, whilst the other could contain a Y-chromosome and an auto-

male \times *grossulariata* female gives *grossulariata* males and *lacticolor* females. Doncaster (1914) found that one mating produced twenty-four *lacticolor* females, no *grossulariata* males, and one gynandromorph, *lacticolor* with the right side of the body male and the left imperfectly developed more like that of the female. The internal genitalia were, as far as was known, imperfectly developed male organs.

The absence of males was associated with an unusual chromosome content in this family (55) for all fertilized eggs lacked a chromosome, the single X passing out into the polar bodies in most cases.

Morgan explains this case as follows.

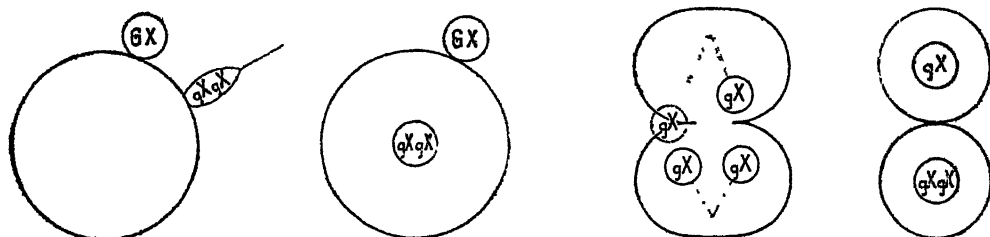


FIG. 6. MORGAN'S INTERPRETATION OF DONCASTER'S CASE

G, gene for *grossulariata*; g, gene for *lacticolor*

some with the gene for zebra. Two sperms of the father carry the X and the autosomal gene for white. Each fertilizing a nucleus would give rise to a male side XX white: white and a female side XY zebra:white. This seems to be the most reasonable interpretation: it demands, as is seen, that the characters zebra and white shall not be sex-linked.

Doncaster's binucleated egg interpretation (Morgan)

Ww XY egg.

WY \times wX = Ww XY female, zebra

wX \times wX = ww XX male, white

(c) *Gynandromorphism in Abraxas*. The characters *grossulariata* and *lacticolor* are typical sex-linked characters. *Lacticolor*

The egg either contains no X-chromosome and therefore no gene for *grossulariata* or else it does contain this X and the gene for *grossulariata*. The male in *Abraxas* is XX. A sperm carrying the *lacticolor* gene-bearing X-chromosome fertilizing the no-X-egg will yield an XY zygote, a female and *lacticolor*. A similar sperm fertilizing an X-bearing egg will yield an XX zygote, a male, and *grossulariata*. Only through the fertilization of a no-X egg by a two-X-bearing sperm could a *lacticolor* male arise. Such a sperm could result from non-disjunction. If the zygote which developed into this gynandromorph was such an XX male (both X's having been derived from the father) then the

gynandromorphism would be due to the elimination of one of these X's at some early division.

Doncaster's second case is one that readily lends itself to interpretation as an instance of chromosome elimination. *Lacticolor* male \times *grossulariata* female gave eleven *grossulariata* males, eleven *lacticolor* females, and one gynandromorph, the anterior parts of which were male and the posterior parts female. The zygote would be an XX individual, one X bearing the gene for *grossulariata*, the other the gene for *lacticolor*. Elimination of a paternal *lacticolor* X-chromosome would give a *grossulariata* male anterior region (XX) and a *grossulariata* posterior region (maternal X).

(f) *Gynandromorphism in Arthropoda, Crustacea, Mollusca, and Echinoderma*. The frequency with which gynandromorphism is recognized in different groups varies with the interest taken by the collector or experimentalist in these groups and with the degree of sex dimorphism that is exhibited. In many forms male and female are very similar in their external characters and in these gynandromorphism will not be detected and in many of the forms in which an occasional instance of gynandromorphism is reported, insufficient is known of the mechanism which in these cases determines sex and models sexual differentiation to allow anything more than a very speculative interpretation being made. It is probable that many cases cited in this connection are not gynandromorphs but are instances of serial intersexuality.

For examples see Kulczynski (1885), Falconer (1910), Hull (1918), Hill (1917), Kuttner (1909), Ashworth (1913), Pelse-n  r (1920), Nichols (1734), Cu  not (1898), D  lage (1902), Herlant (1918).

(g) *Gynandromorphism in birds*. Since gynandromorphism is the result of an

abnormal functioning of a mechanism it cannot be the normal characterization of a group. It can only affect those tissues the cells of which pursue their differentiations independently of all others. It is, therefore, impossible to find a gynandromorph in those groups in which the control of the processes of sexual differentiation has been completely relegated to some special organ or tissue; it cannot occur in the mammal if in this group sexual differentiation is mainly pursued under the directing stimulus of a sex-hormone elaborated by the differentiated gonad. If in a group, undoubted, and otherwise inexplicable, cases of gynandromorphism are found, then in that group the internal secretions of the gonad do not constitute the sole controlling forces in sexual differentiation and the cells of different parts can pursue their differentiation under the direction of their own genotype.

Gynandromorphism has been recorded in birds. Poll (1909) described a true bilateral bullfinch; Weber (1890) a finch (and refers to two other cases described by Cabanis, 1874); and Bond (1913) a pheasant. In the finches the right side of the body was male and the gonad a testis, the left female, and the gonad an ovary. In Bond's pheasant the left side of the body was male, the right female, and the gonads were ovotestes. The individual tail feathers had one half of the vane with male markings, the other half with female. Macklin (1923) describes a fowl (breed not stated) which had the plumage characterization of a hen with neck-feathering suggestive of that of the male and with tail sickles rather longer than those of the normal hen. (It will be shown later that this tail characterization is associated with the synchronous presence of both ovarian and testicular tissues in experimental birds, either male

or female, and that it is the normal condition in the Campine henney-feathered cock). The comb and right wattles were as those of a cock, and the bird exhibited male behavior, attempting copulation with hens with apparent success. It was not known to crow and it did not fight with cocks. It was known to be laying, but since it was suspected of laying small eggs it was killed. When it was being prepared for the table it was noticed that the right side of the body was distinctly larger than the left and that there was a testis on the right and on the left an

centered in the gonads. In a male zygote one X-chromosome was eliminated at the first cleavage division of the fertilized egg, or according to the grade of femaleness in the characterization, later at some division of a cell in those areas which are to be involved in the sexual characterization. Evidence in support of the hypothesis that aberration in the distribution of the sex-chromosomes can occur in the somatic cells is to be obtained from a study of the abnormalities in the distribution of sex-linked plumage color characters. Serebrovsky (1925) explains the

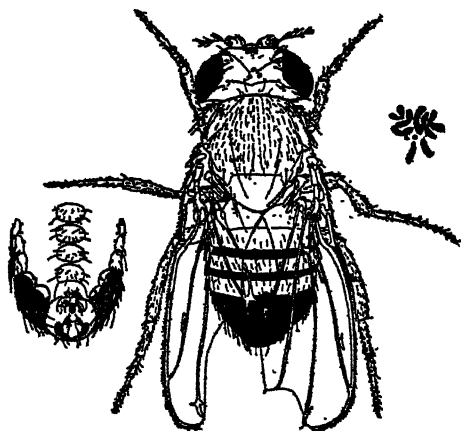


FIG. 7A

FIG. 7A. MALE TYPE INTERSEX ($2X:3A-IV$) (FROM MORGAN, BRIDGES AND STURTEVANT)

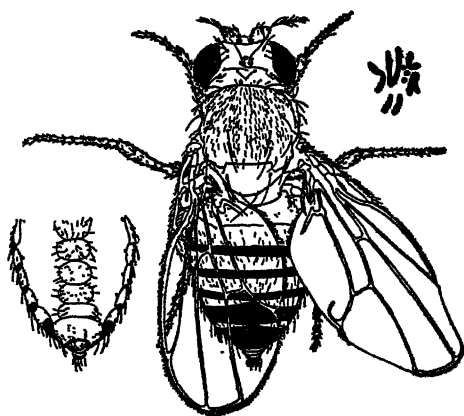


FIG. 7B

FIG. 7B. FEMALE TYPE INTERSEX ($2X:3A$) (FROM MORGAN, BRIDGES AND STURTEVANT)

ovary (which really was an ovotestis) and an oviduct. The histological examination showed that it could have laid and that there were normal looking spermatozoa and a testis of normal appearance. Every bone on the right side was larger than the corresponding bone on the left, these latter being 66 per cent as heavy and 85 per cent as long.

These cases can best be interpreted as gynandromorphs in a group in which the male is monogametic (XX) and in which the control of the processes of sexual differentiation is not absolutely

occurrence of black feathers in a barred silver plumage by postulating that in the cells in which these feathers have their origin, the sex-chromosome, in which the sex-linked factors for barring and for silver are resident, is lost during its transference from mother to daughter cells. The question of the presence of ovotestes in these cases will be discussed later.

2. *Balanced intersexuality in Drosophila melanogaster.* The $2X:3A (-IV)$ male and the $2X:3A$ female intersexes. In an experiment made by Bridges (1921) to deter-

mine the locus of a new second chromosome recessive mutant "brown" by means of a back-cross to plexus and speck, one culture produced 96 females, 9 males and about 80 individuals which were abnormal in their sexual characterization. These intersexes were large bodied, coarse bristled flies with large roughish eyes and scoloped wing margins. The intersexes showed a bimodal variation, one group more closely approaching the female in

the abdomen and genitalia was predominantly male. Sex-combs were always present. The gonads were typically rudimentary testes though in a few cases the testes were well developed and contained bundles of sperm.

Moreover, instead of getting but two classes of offspring among the progeny of the back-cross as would be expected, three classes appeared, plexus speck, plexus brown, and brown speck. This unex-

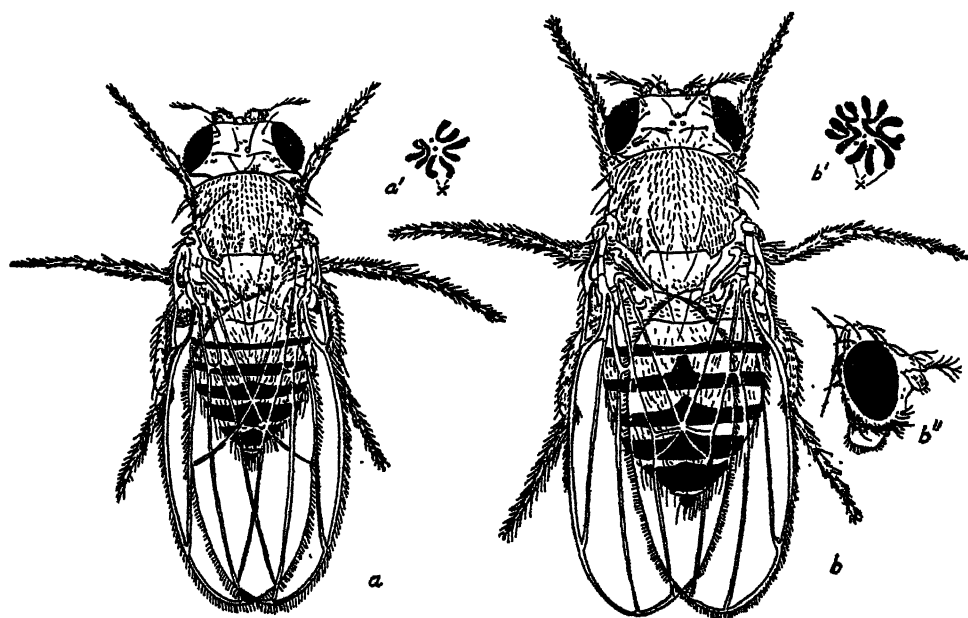


FIG. 8. *a*, NORMAL FEMALE, *b*, TRIPLOID (3N) FEMALE. *b''*, THE LARGE ROUGH 'EYE' (FROM MORGAN, BRIDGES AND STURTEVANT)

characterization, the other the male. All were sterile. In the female type the genitalia were predominantly or completely female, the abdomen was very much as that of the normal female: spermathecae were present. The gonads were typically rudimentary ovaries: in many cases the ovarian tissue had a bud of testicular tissue, in others one gonad was a rudimentary testis, the other a rudimentary ovary. Sex-combs were usually present. In the male type, the characterization of

pected result can only be explained on the understanding that the mothers had three instead of two chromosome II, one carrying plexus brown, one plexus speck, and one brown speck. From their father each had received a chromosome II carrying plexus, brown, and speck, and from the mother they had received one of the three kinds of chromosome-II mentioned. She had two genes for each of the recessive characters, plexus, brown, and speck, and one for each of the alternative dominants.

Further tests showed that the mothers were also triploid in respect of chromosomes I and III whilst chromosome IV was present either in the duplex or triplex state. It was noticed that these $3N$ (where N = the haploid chromosome number) mothers could be distinguished from the ordinary normal female by their large size, coarse bristles, and rough eyes. That the intersexes were themselves triploid and not diploid with respect to chromosome II was shown by the fact that the classes, with respect to plexus, brown, and speck, among them were strikingly different from those in the sexually normal males and females. The

It is to be noted that the infecund female type of intersex differs from her very fecund mother in that she is $2X:3A$ whereas the mother is $3X:3A$, and that in these intersexes the addition of a fourth chromosome makes all the difference between a male type and a female type.

For the production of these intersexes polyploidy must have occurred in earlier generations. Bridges has shown that in certain cases ordinary diploid females possess ovaries in which there are areas the component cells of which are much larger than the normal and that in these the chromosomes are tetraploid ($4N$). Evidently in some oogonial cell there had

TABLE 2

CHROMOSOME RELATION	SEX TYPES	NUMERICAL RATIO X (100) A (80)	SEX INDEX	INTERVAL	X = -6 A = +2
				per cent	
$3X:2A$	Super-female (triplo-X)	1.5 : 1	1.88	50	-14
$4X:4A$	$4N$ female	1 : 1	1.25		-20
$3X:3A$	$3N$ female	1 : 1	1.25		-12
$2X:2A$	$2N$ female	1 : 1	1.25		-8
$1X:1A^*$	$1N$ female	1 : 1	1.25	50	-4
$2X:3A$	Intersex (female type)	1 : 1.5	0.83		-6
$2X:3A$ (-IV)	Intersex (male type)	1 : 1.5	0.83	33	-6
$1X:2A$	Male (normal)	1 : 2	0.63	50	-2
$1X:3A$	Super-male (triplo-A)	1 : 3	0.42		-0

* This type has only recently been described (Bridges, 1926).

intersexes presented three classes also but these were plexus, speck, and brown respectively.

It was readily possible to put this explanation of triploidy to the test of cytological examination and it was found that all the intersexes carried two X-chromosomes, three of each chromosomes II and III. Certain of them carried a Y-chromosome and some of them had three IV's, others two. It was thought at first the triplo-IV's were the male type, the diplo-IV's the female type of intersex, but further investigation has shown that this is not so; the triplo-IV's are the female intersexes, the diplo-IV's the male.

been chromosome division of the nucleus so that all mature eggs would be diploid. The same process could occur in spermatogenesis. Should such a diploid gamete fuse with a normal haploid gamete from the mother parent it would give rise to a $3N$ zygote.

The following represents the series of sex types in *Drosophila melanogaster*. If the efficiency of the female determining genes (X-borne) is represented as 100 and that of the male determining gene-complex in the autosome as 80, a series of sex-indices can be made. (See table 2).

A review of these facts supports the contention that the initial sexuality of

the zygote is determined by the interaction of the genes resident in the chromosomes, sex-chromosomes, and autosomes alike. The addition of more autosomal chromatin (= autosomal-borne genes) to the usual female $2X:2A$ balance so disturbs this that the relationship is now that which can be expressed as $2X:3A$ and results in the establishment of a physiological state in which male type characters develop, i.e., the addition transforms a female type of metabolism into one which approaches that characteristic of the male. The addition of more X-chromatin (= X-borne genes) to the usual male $1X:2A$ balance so disturbs this that the relationship is now that which can be expressed as $2X:2A$, one that is typical of the female.

There can be no doubt that it is far simpler for purposes of discussion to assume that in the X-chromosomes are genes that are "female-determining" and that on the autosomes are genes that are "male-determining" and that the sexuality of the zygotes is determined by the balance between these. For example, if F is taken to represent a set of such female-determining genes on an X-chromosome, if M indicates a set of the male-determining genes in one set (haploid) of the autosomes, and if in their relationship $1F$ is greater than $1M$ but less than $2M$, then in those classes in which the male is digametic

(FX) (FX)MM is a female because $2F > 2M$

(FX) Y MM is a male because $1F < 2M$

In the classes in which the female is digametic it is necessary to place the male-determining genes on the X and the female determining genes on the autosomes,

(MX) (MX)FF is a male because $2m > 2F$

(MX) Y FF is a female because $1M < 2F$

and in either case in those circumstances in which the quantitative balance between

the male and the female determining genes is such as to lead to a situation in which $M = F$, intersexuality will result.

But it is to be understood that this is but a way of explaining an imperfectly understood subject concerning which there is a profound lack of physiological knowledge. It would appear to be an established fact that in *Drosophila* the effective factor in the establishment of maleness, femaleness, and intersexuality is the numerical ratio of X-chromosomes to autosomes. Underlying the above explanation is the difficulty that as yet actual differences, as estimated by differences in the chemical nature of the products of their functioning, undoubtedly exist in different types of chromatin organization (genes) and in different gene associations (chromosomes). The chromatin of the X-chromosome is physiologically different from that in the autosome but as yet this difference cannot be defined. At present all that can be stated is that the difference is such that more or less X-chromatin (and also of IV chromatin) in association with more or less A-chromatin leads to one of three types of internal environment in the zygote and its cells, maleness, femaleness, and intersexuality.

In a yellow stock of *Drosophila melanogaster*, L. V. Morgan (1925) found an individual in which the two X-chromosomes were joined end-to-end and from this a stock was raised. It will be seen that so long as this double-X remains unbroken such a female will elaborate two sorts of egg, one carrying the double-X and the other lacking an X. A double-X egg fertilized by an X-bearing sperm will yield a triplo-X super-female. The same egg fertilized by a Y-bearing sperm will yield an XXY female. This double-X chromosome, however, is liable to break at any point along its length. Mul-

ler and Dippel (1926) have shown that by exposure to X-rays artificial breaks of this chromosome can be caused, and that under these circumstances the break is at or near the point of juncture of the two X's. Natural breakage results in a J-portion longer than the normal X and a shorter portion which, owing to the fact that it includes no points of attachment for the spindle, is lost. The XXY female will elaborate XX:Y:J ova. The J-bearing ovum fertilized by a Y-bearing sperm yields a normal male.

Muller and Dippel point out that during

derived from an earlier period in which they possessed the female gene complex, but because, they would suggest, the processes of oogenesis really—chemically—begin in much earlier germ cells than the oocytes and that after the early period in which oogenesis is initiated, each step in the process in turn produces the next reaction of the series in chain-like connection until the definitive ova are laid down without the further direct intervention of the genetic determiners that decided the nature (whether male or female) of the original reactions.

TABLE 3

	MALES	FEMALES	INTERSEXES
Sex combs on forelegs.....	Present	Absent	Absent
Number of dorsal abdominal tergites.....	Five	Seven	Seven
Ovipositor.....	Present	Absent	Present
Spermatheca.....	None	Two	Two
Penis.....	Present	Absent	Absent
First genital tergite.....	Present	Absent	Present
Anal plates.....	Lateral	Dorsal	Lateral
Claspers.....	Present	Absent	Present
Tip of abdomen.....	Black	Banded	Black
Gonads.....	Testes	Ovaries	Very minute
Sex-chromosome constitution.....	XY	XX	XX (even those parts with male characterization)

the course of the elaboration of these ova there were involved tissues which possessed an XY type of genotype like that which occurs in ordinary diploid male cells, and like the spermatogonia themselves, and they express surprise that cells of identical genetic composition and in an identical environment may thus pursue entirely different modes of development. They point out that cells of male genetic composition metamorphose into ova not because of any special substance or influence exerted upon them derived from other cells of the female body, and not because of any egg-forming substances that might be present within their own protoplasm,

It will be argued in this paper that the form of the gamete is determined by the organization of the gonad, this being determined by the initial general or local genotype, and that the genotype of the gamete has no relation to its form or function.

B. Disharmony in the composition of the genotype

1. A "gene" for intersexuality in *Drosophila simulans*. Sturtevant (1920) has shown that there is a single recessive chromosome II gene which when in the duplex state turns females into intersexes and renders males sterile. Two hundred

of these intersexes appeared in a stock and unlike the rather variable polyploid intersexes of *Drosophila melanogaster* were all of a definite and constant type. Their characterization is detailed in table 3.

Matings between the stock that gave the intersexes and others that did not, gave no intersexes in F_1 , but these appeared in F_2 . Pair matings within the intersex-producing stock gave 510 females; 165 intersexes; and 754 males, an excess of males and a 3:1 ratio in respect of sexual normality and sexual abnormality. This character intersexuality is linked with the chromosome II recessive character plum, for three F_1 females out of an intersex \times plum mating gave in F_2

<i>Females:</i>		
Wild type	Plum	
198	91	
<i>Intersexes:</i>		
Wild type	Plum	
87	0	
<i>Males:</i>		
Wild type	Plum	
293	65	

There was no intersex plum class, showing that these characters are linked, that their genes are resident in one and the same chromosome.

These cases are of the utmost importance in that they show that intersexuality can be caused by a genetic and stable reorganization of the chromatin in a single locus in a chromosome and that this in its effects is sufficient to transform the state of femaleness which would have become established in its absence into one of stable intersexuality. It is of interest to note that the duplex state of the gene is required to produce this result in the female, whereas in the male it leads only to a genetic type of infecundity. It should be understood that by a gene for intersexuality is meant that a certain organization of the chromatin in a particular area of a particular chromosome, different from that organization of the chromatin in

this area that is associated with the development of a normal sexual characterization, produces in its action, through its physiological contribution to the general economy of the zygote, a disturbance in the internal environment so that this no longer is characterized by those properties which can be summed up as femaleness but becomes altered in the direction of maleness.

It will be noticed that certain of the component structures of the sexual characterization of the intersex are completely female and that others are completely male. There is no intermediate characterization of parts. That this is so might conceivably be explained in one of two ways. The zygote is a genotypic female 2X:2A in chromosome constitution but on two of the autosomes there is the gene for intersexuality. Every cell of the body will contain the same genotype. The internal environment of every cell is the same yet some tissues differentiate according to the architectural plan of the male, others to that of the female. It may be that certain tissues are more susceptible to the stimulus of the modified environment. But another explanation and one that seems to be more reasonable is that which assumes that there is a time seriation in differentiation, those structures that assume the male characterization becoming differentiated earlier or later than those that assume the female characterization, and that the gene for intersexuality comes into action when one or other set has completed this differentiation. The intersexes would then be intersexes in time. The suggestion that all the component genes in a genotype do not come into action is not extravagant; it is more pleasing than that which demands a varying potency of genes. The conception that the genotype is to be regarded as an unbolting mechanism, the units of which come into action serially

and evoke responses in tissues that exhibit a seriation in the time at which they can respond will be discussed later.

2. *Serial Intersexuality in Lymantria*. It has long been known (Standfuss, 1896) that when species or even geographical races of Lepidoptera are crossed sexual abnormalities commonly are found among the hybrid offspring. For example, if European specimens of the notorious forest pest, *Lymantria dispar*, the gipsy moth, are bred among themselves the offspring are unremarkable in every way. The same is true in the case of the Japanese variety, *Lymantria japonica*. But if a Japanese male is mated with an European female, normal male offspring and females that show a number of modifications in the direction of maleness, i.e., females that are intersexual, are produced. When such female intersexes were fecund, i.e., were not too abnormal, and were mated with their brothers, it was found that in the succeeding generation typical Mendelian segregation occurred, half the females being sexually normal, half being intersexual. The reciprocal cross, European male and Japanese female, produces normal males and females in the first cross-bred generation, but if these are then interbred there appear in F_2 a certain proportion of males that show modification in the direction of the female type of organization, i.e., males that are intersexual.

Further investigation by Goldschmidt (1923) and his associates demonstrated that there were many different races of European, Japanese, and American gipsy moths that were quite distinct in their hereditary constitution in respect of this character intersexuality, in that the degree or grade of intersexuality was definite and typical for a particular mating. As the result of much experimental breeding work Goldschmidt was able to classify

his strains as relatively "strong" or "weak." For example, a "strong" male mated to a "weak" female would give 50 per cent normal males and 50 per cent intersexual females. A very "strong" male mated to a "weak" female would give offspring all possessing the male type of sexual organization. A mated to B gave low grade of intersexuality, $C \times D$ a high grade, $E \times F$ a grade intermediate between these, and so on. If strong race A gave moderate intersexuality with weak race P, while with race Q it gave strong intersexuality, and if strong race B gave moderate intersexuality with Q then it could be predicted that B with P would give only a slight grade of intersexuality. Similar males from one culture mated with females from different cultures gave intersexes that could be arranged in a series according to the degree of their abnormality: males from different cultures mated with females from one and the same culture gave intersexes that differed from these but which could also be arranged in a series. It was possible, by calling on experience, to produce at will every stage from an almost complete male to an almost complete female intersex by making the appropriate mating. In fact, it was as possible to turn the genotypic females into phenotypic males as to ensure the regular production of normal males and females.

It was noticed that the condition of intersexuality did not affect all the structures of the sexual organization equally. Some were normal, while others were intersexual in their characterization, and only purely quantitative characters, such as the length of the antennal pennae, exhibited a condition intermediate between those of the normal male and female. Further investigation demonstrated that the different structures could be arranged in a definite series as regards de-

velopment of intersexuality in characterization and that this series was exactly the opposite to the order of the embryonic differentiation of these structures. Those organs which are the first to be developed and differentiated are the last to be modified; those that appear last are the first to be changed. From these considerations there arose the Time Law of Intersexuality. An intersex is an individual that has developed as a male (or female) up to a certain point in its life history and thereafter has continued its development as a female (or male). The degree of intersexuality is determined by the time during the critical period of sexual differentiation at which this switch-over occurred.

The intersexual females start their development as females and then at a certain point in their development change their mode of differentiation and finish as males and since the hard parts of an insect are external and composed of chitin any of them that have hardened before the switch-over remain unaltered by it. From an examination of the parts which are sexually dimorphic, it is possible to decide in the case of any particular individual exactly when the change-over took place. The intersex is a sex-mosaic in time. The female showing the least degree of intersexuality has only the feelers modified in the manner of the "feathered" male type. Those displaying a further degree of intersexuality will have the male coloring of the wings in addition. A further stage will consist in the addition of a male type of copulatory organs. Next will be a male-type abdomen, and the final stage of all will be that in which the ovaries are replaced by testes, i.e., the genotypic female (according to chromosome content) will have become a phenotypic male, i.e., an XY individual has assumed the characterization normal in one with the XX type of chromosome

constitution. The fact that an individual primarily equipped with ovaries can become so transformed as to possess testes is of profound interest since it illustrates in the clearest possible manner the relation of the structure of the gamete to the organization of the individual producing it. Genotypically the sperm will be identical with the ova previously produced but structurally and physiologically they will be profoundly dissimilar. The genotype of the zygote decides the organization of the gonad and this decides the morphological and physiological properties of its manufactured product, the egg or the sperm. It is not the genotype that distinguishes egg from sperm; they differ because they are the products of dissimilar gonadic organizations and the difference takes the form of dissimilar structure and behavior.

From these facts Goldschmidt deduced the following conclusions:

(1) Each sex possesses the potentialities of the other since either can become intersexual. (In other words, the embryonic tissues are ambivalent as regards their future sexual differentiation).

(2) The type of sexual differentiation that the zygote will pursue is determined at the time of, and by the mechanism of, fertilization. (In other words, sex is determined by the nature and interaction of the genotype established in the zygote by the conjugating genes. If the genetic ingredients of intersexuality are in the zygote, then the individual will inevitably become an intersexual form).

(3) The normal determination of sex is bound up with the X-2X mechanism. But as this does not prevent the occurrence of intersexuality and the transformation of one sex into the other, it cannot be the mere presence of these chromosomes or the factors contained within them that counts, but rather their quantitative effect.

(This is in line with the conclusions that have emerged from the consideration of other forms of intersexuality discussed earlier in this paper).

(4) The mode of inheritance of this intersexuality shows that since the female in *Lymantria* is XY, and since her single X-chromosome is received from her father, one of the deciding factors in sex-determination is transmitted in the X-chromosome. (This is in line with previously formed conclusions).

(5) Other factors concerned in sex determination in *Lymantria* are purely maternal in inheritance, being resident in the Y-chromosome. A daughter receives her Y-chromosome from her mother. But since a male has no Y-chromosome, the factors in the Y-chromosome must have exerted their action on the unripe egg when this contained both X- and Y-chromosomes. (It will be remembered that the mature egg of a female that is digametic carries either an X or the Y. This is due to the fact that of this XY pair one member passes into the polar body whilst the other stays in the egg. The eggs will therefore be of two sorts, X-chromosome bearing and Y-chromosome bearing, the former being fertilized by the X-chromosome bearing sperm and giving rise to an XX individual, a male, the latter being fertilized, to an XY zygote, a female). If all eggs are to be alike in respect of the Y-borne genes these must have acted and their products must have specifically affected the cytoplasm before the X and Y became disjoined. It is seen then that there is good reason for postulating that different genes come into play at different times. It is to be noted that the Y-chromosome of *Lymantria* is not as the Y of *Drosophila*, it is not physiologically inert but resembles the Y of fishes in that it carries active genes (Aida, 1921, Winge, 1922).

(6) The fact that the genetically similar females give different results when mated with genetically dissimilar males shows that the sex-determining genes in the X-chromosome differ quantitatively in the different races. The fact that genetically similar males give different results when mated with genetically dissimilar females shows also that the sex-determining factors resident in the Y-chromosome can be different quantitatively.

It will be seen that if both X-borne and Y-borne sex-determining genes can so vary quantitatively among themselves an infinite variety of different genetic combinations can be made, deliberately or by chance.

In order to explain his results and his hypothesis Goldschmidt developed a somewhat intricate presentation. To the male-determining tendency of a particular race he assigns a positive value that is proportional to the strength of the male-determining genes. To the female-determining tendency he assigns another value also proportionate to the strength of the female-determining genes. He then assumes that when in an individual the male value is greater than the female value by a certain number of units the individual is a male and that conversely when the female value is greater than the male by a certain number of units the individual is a female ($F - M = > 20$, a female; $MM - F = > 20$, a male). In a weak race, for example, F, the female-determining gene complex, has a value of 80 units assigned to it and M has 60. Since the male-determining gene-complex M is borne on the X-chromosome and the female-determining gene complex F is in every egg in the female, XY in constitution, F 80 exceeds M 60 by the epistatic minimum of 20 units, and the individual therefore becomes a female; in the XX

males, on the other hand, $M = 60 + 60$ as against $F = 80$, so that there is an excess of 40 units in the male direction. In a strong race F is 100, M is 80, but the arithmetical relation between the values of F and M still governs the sexuality of the individual. (It should be stated that it does not seem impossible to restate the whole argument in terms of a numerical ratio as Bridges has done in the case of *Drosophila*. This algebraic interpretation is not really satisfactory).

since they come from different sources (see table 4).

By the use of such symbols it is easy to illustrate the production of an F_1 generation consisting of 50 per cent males and 50 per cent females whose bodily characteristics are male (see table 5).

Goldschmidt infers with reason that the sexual characterization of any particular organ of the sex equipment depends on whether one or the other type of sex-differentiating substance is effectively in

TABLE 4
RECIPROCAL CROSS

A weak male.....	$M_2M_2F_2$	M_2mF_4	A strong female	
Gametes.....	M_2	$M_2F_4 : mF_4$		
F_1	$M_2M_2F_4$ $M > F$ therefore ♂	M_2mF_4 $M < F$ therefore ♀		
Gametes.....	$M_2 M_2$	$M_2F_4 mF_4$		
F_2	$M_2M_2F_4$ Intersexual male	M_2mF_4 Female	$M_2M_2F_4$ Male	M_2mF_4 Female
	$M = F$	$M < F$	$M > F$	$M < F$

> = greater than; < = less than.

TABLE 5

P_1 , strong male.....	$M_5M_5F_5$	M_2mF_3	Weak female
Gametes.....	M_5	$M_2F_3 mF_3$	
F_1	$M_5M_2F_3$ Male $M > F$	M_2mF_3 Female (MmF) but $M > F$, so all with male organization	

The conception of Goldschmidt can be illustrated by assigning arbitrary numerical symbols to the sex-determining factors. M = male-determining gene resident on the X-chromosome. M_1, M_2, M_3, M_4, M_5 , etc. are male-determining genes of relatively different efficiencies; M_1 is a weak M , M_5 a relatively very strong M , and so on. Since a male has two X-chromosomes he carries two M 's and these may be of different grades of efficiency,

excess at the time when the organ arises in development. He interprets the mosaic character of the intersex by the assumption that the amount of sex-differentiating substances produced in virtue of the presence of the corresponding sex-determining genes is not constant throughout life: that at one time the male-differentiating substance is in excess, at another the female. In the male of the moth $M > F$ and the male-differentiating substance

is effectively in excess until the period of differentiation is completed. In the case of the female $M < F$ and the female-differentiating substance is effectively in excess during development. But if it should so happen that the sex-differentiating substances are produced at different rates, and if some genes possess the property of producing more sex-differentiating substance in a given time than others, then there

The male offspring, on the other hand, will receive one M from their mother, and the other, the quickly producing M , from their father, so that in a given time the male-differentiating substance will be effectively in excess during development. The female offspring will have the M from the father, and as a consequence the amount of male-differentiating substance will increase relatively to the

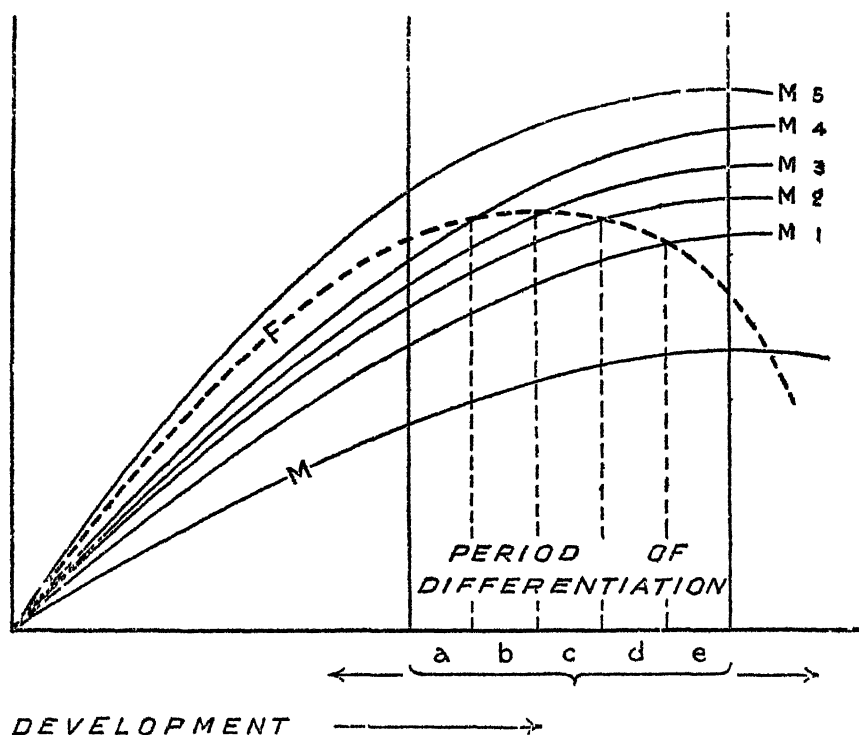


FIG. 9. THE TIME LAW OF INTERSEXUALITY (AFTER GOLDSCHMIDT)

exists the possibility that sex mosaics in time will be produced.

A male of a race in which the sex-determining genes work at a faster rate is crossed with a female of a race in which these genes work at a slower rate. The female-determining factor F is always inherited through the mother and in all the offspring there will be this factor F and the female-differentiating substance

amount of the female-differentiating substance, overtake it, and finally supplant it, and from this point onwards any sex-characters which still have to develop will be of the male type. The individual will be a female intersex. It is not the absolute but the relative rates of production of male- and female-differentiating substances that control the modelling of the sex-equipment, as shown in Figure 9.

genes, male-determining, borne on the X, and female-determining, borne on the Y. The male genetically is MMF and the female MmF, since the action of the Y-borne genes is prezygotic. The sex-determining substances elaborated by these genes are known as male-differentiating and female-differentiating substances. These are elaborated at different rates by different male-determining and female-determining genes respectively; the introduction of more quickly and of more slowly elaborating genes into a genotype can result in a disturbance of the previous quantitative relation of the two sorts and so yield the intersexual condition.

In general the point at which the curves for production of the male- and of the female-differentiating substances intersect lies beyond the stage at which differentiation occurs. But if the growth rate could be changed so that the point of intersection occurred during or before the period of differentiation, then it should be possible to produce a partial or complete reversal of sex and to produce individuals genetically of one sex (XX or XY, that is), but somatically, phenotypically of the other. Goldschmidt by rearing *Lymantria* at very low temperatures produced intersexes, thus verifying this inference. Sex-reversal in these cases is due to genetic causes—the fertilized egg contains inevitably within itself the seed of its eventual transformation in the form of a quantitative disharmony of the sex-determining factors.

In the case of *Lymantria* the situation can be summarized as follows. Genetic intersexuality is the condition in which as a result of genetic causes the differentiation of the sex-organization of a genotypic male or of a genotypic female, having been pursued up to a point in a manner appropriate to that sex, is switched over, so that after this point it follows the plan

appropriate to the opposite sex. An intersex is an XX (or XY) individual which, as a result of an abnormal sexual differentiation comes to possess more or less completely the sex equipment appropriate to the alternative XY (or XX) individual. Not every part of the body is involved in this condition; only the structures of the sex equipment are concerned and of these only those are affected the differentiation of which is not complete at the time of the switch-over; the earlier in development the switch-over occurs, the more structures will be affected and the greater will be the degree of the intersexual condition, and *vice versa*.

Intersexuality results when the male and female sex-determining genes are quantitatively incorrectly in harmony, one set with the other. It does not occur when, as in the case of the genotypic female which attains a typical female organization, the female-determining reactions are predominant throughout the period of differentiation. Intersexuality occurs when during the course of this phase of differentiation the male-determining reactions overtake and supplant the female-differentiating reactions and so control the remainder of the process, or when the female-differentiating reactions replace the previously predominating male reactions.

Under ordinary circumstances the female sex-differentiating substances in the male or *vice versa* are produced so slowly that an effective quantity is not present until the critical phase of differentiation has closed. If, however, their production were speeded up through the presence and action of a more rapidly producing female gene-complex, the time point at which these female-differentiating substances attained effective supremacy would fall within the critical period of differentiation and would then be the switch-over point. Each fertilized egg normally pos-

sesses male and female-determining genes which elaborate enzyme-like and specific sex-differentiating substances. In species in which the female has the constitution symbolized as XY, the female sex-differentiating substances are purely maternal in their mode of transmission so that every egg produced by one and the same female is identical in respect of this. The male-determining gene-complex is X-borne, and, therefore, is present in half the eggs and in all the sperm. The rate of production of the two sex-differentiating substances or the time at which they come into action is a fixed hereditary character of a race.

The case of *Lymantria* is of particular interest because it provides strong evidence that there are genes on the Y-chromosome and that different genes come into action at different times during development. It is seen that in *Lymantria* the Y-borne genes are not concerned with the development of morphological characters directly but with the establishment of a certain metabolic level. In the case of *Drosophila* it is known that the Y-chromosome is not concerned in the development of morphological characters but that its presence is necessary if the male is to be fecund. It is possible that the Y-chromosome of *Drosophila* does carry genes and that these, like the Y-borne genes of *Lymantria*, are concerned with the establishment of physiological characters exerting their action before organogenesis commences.

It is important to note that though the phenomena of intersexuality in *Lymantria* are commonly interpreted as the results of genetic difference in the rate of production of sex-differentiating substances, it is equally satisfactory to explain them as the sequelae of genetic differences in the time at which different gene complexes concerned in sex-determination come into

action during development. M_1 and M_5 would then be equally potent, but M_5 would come into action earlier. In this connection the work of Hartmann (1925) on the plant *Ectocarpus siliculosus* is well worthy of reference.

The researches of Pflüger (1882), Hertwig (1912) Schmidt-Marcell (1908), Kushakevich (1910) and Witschi (1914-1915) have revealed the fact that in the frog there are two forms of development of the reproductive organs. In one the differentiation of the gonad is either that which leads directly to the organization of an ovary or that which directly yields a testis. In the other there is in the beginning an organization that is female in its characterization but sooner or later 50 per cent of these cases become transformed into testes. It has been established that this tendency to early and direct differentiation on the one hand, and to late and indirect differentiation on the other are truly heritable characters and that the hereditary factors for these characters can be transmitted by either father or mother; breeding experiments yielded results closely resembling those obtained in the mating of individuals of different "efficiencies" of *Lymantria*, and there is good reason for interpreting these temporary intersexuals in terms of Goldschmidt's *Lymantria* hypothesis. Swingle (1925) very ably upholds the view that the early gonad of the male of indirect and late differentiation is not ovarian and that such a male is not an intersexual. He argues that this progonad is sexually neutral in consequence of a balance between male and female determining tendencies in the zygote and the fate of the progonad is decided when the definitive sex-cords appear, for then the progonad becomes transformed into a testis. The definitive testis cannot develop in the absence of sex-cords and the appearance

of these decides the course of development. The time of the appearance of these peculiar male structures, the sex-cords, is probably determined by genetic factors and so different races and their hybrids differ in the time at which progonad becomes testis. According to Swingle "Pflüger's hermaphrodites" are but males in which the appearance of sex-cords in the progonad is greatly retarded and many recorded cases of sex reversal in the frog and toad are but instances of such retardation.

It is of considerable interest to note that Witschi secured an adult hermaphrodite the eggs and sperms of which were used. The eggs of this hermaphrodite fertilized with sperms from an individual of a race in which early and direct differentiation was the rule yielded males and females: sperms of the hermaphrodite fertilizing eggs of a female of a race in which early and direct differentiation was the rule gave only females. These facts point to the conclusion that this hermaphrodite frog was XX in sex-chromosome constitution and that all its gametes, eggs and sperms alike, contained a single X. The X sperms fertilizing the X eggs of the monogametic female yielded only XX individuals: the X eggs being fertilized by both X and Y sperms gave both males and females. It is to be noted that here again is an instance of egg and sperm being genotypically equivalent, of ovary and testis being possessed of the same genotypic constitution. Manifestly though an individual that has the sex-chromosome constitution XY develops testes, these develop not because they are XY but because they developed in a particular kind of internal environment that the interaction of the genes in an initial XY genotype established.

Hertwig and Witschi were able to show that temperature has a definite influence on the type of gonadic differentiation in frogs.

They found that certain forms cultivated at 21°C showed early and direct gonadic differentiation, whereas when cultivated at 27°C some of the females changed after the metamorphosis into males. In another race cultivated at 27°C all these females became transformed into males. Evidences of this transition in sexual differentiation can be obtained from other sources. At the anterior end of the testis of the toad is Bidder's organ, a rudimentary ovary. It is found in both sexes while the individuals are immature but in the case of the female it degenerates. Harms (1914) was able to show that Bidder's organ was a rudimentary ovary and that it possessed an endocrine function. All the males of *Perla marginata* possess a well developed but non-functional ovary anterior to the testis (Schönemund, 1912). In *Phyllodromia germanica* Heymons (1890) has demonstrated that the anterior part of the gonad of the male is differentiated into ovarian tissue; in *Orchestia Nebeski* (1880) has shown that a part of the testis always contains eggs; while in the crab, *Gebia major*, Ischikawa (1891) has shown that the anterior part of the gonad of the male is testicular whereas the posterior portion is ovarian though incapable of functioning. In *Myxine* Schreiner (1904) has shown that while no real hermaphroditism occurs, the gonad is mixed, though only the testicular or the ovarian tissue is functional. The work of Grassi (1919) on the eel suggests that similar conditions obtain in this form.

These and many other cases can be interpreted by an appeal to the hypothesis of Goldschmidt.

If it is agreed that the essential difference between the male and the female lies in the timing mechanism which decides whether, while a given organ is developing, the male or the female

determining reactions are predominant, if it is agreed that at some point in the development preceding or following the stage of differentiation the female determining reactions are predominant in a genotypic male and *vice versa*, then the efficiency of environic agencies to co-operate with the genetical factors offers no difficulty. The provisional hypothe-

Bidder's organ, for example, can readily be interpreted on Goldschmidt's hypothesis. A represents the progonad; B the definite testis. It will be remembered that the development of the progonad is actually later in the forms with a protracted larval phase. During the earlier part of the development of the individual the female-determining reactions are pre-

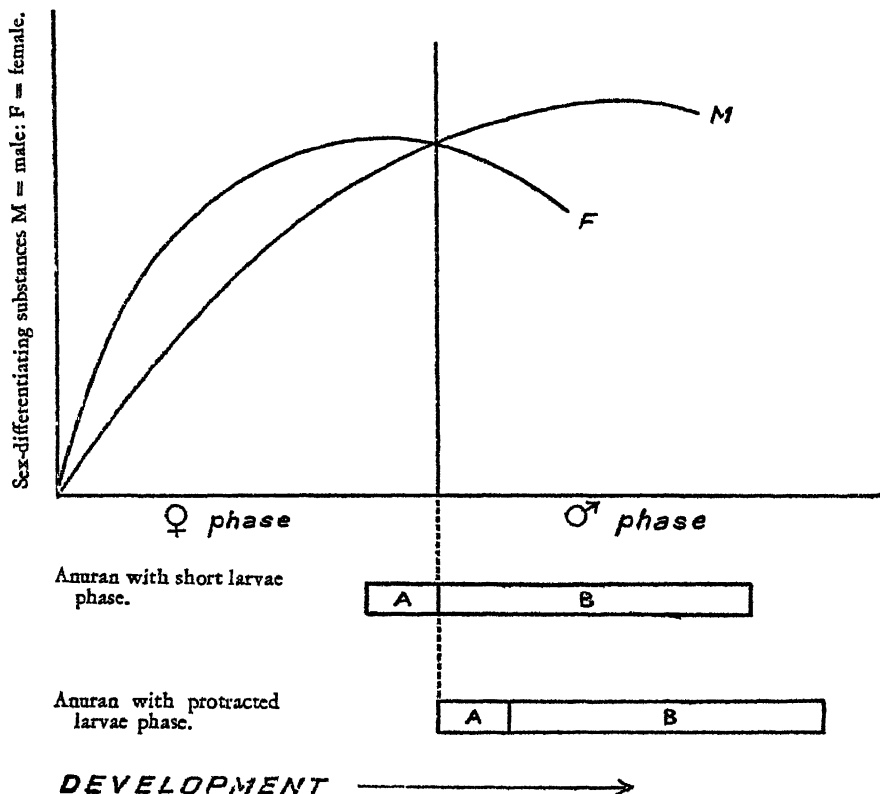


FIG. 10

sis outlined by Goldschmidt to account for his *Lymantria* intersexes then brings into one coherent scheme undoubted sex-transformation as seen in *Crepidula*, *Sacculina*, and *Bonellia*, the occurrence of oviform cells in the protestis of *Anura* (or among Myriapods as steps in normal spermatogenesis), and the cases of sex-reversal met with in birds.

Fig. 10 shows how the significance of

dominant, the female-determining substances are effectively in excess, and any organ that is developed during this period and is responsive to the action of their stimulus will pursue its development and differentiation under their direction; later, in the case of the determined male, the male-determining substances become effectively in excess, and all differentiation of the structures of the sex-organization will

thenceforward be according to the male plan. Thus it will happen that in the case of the Anuran with a short larval phase, the progonad will present the characteristic features of Bidder's organ, whereas in the case of the Anuran with a protracted larval life, in which the progonad is developed later, there will be no Bidder's organ and no ovum-like bodies in the testis.

Other somewhat similar instances of intersexuality that must await interpretation until it has been shown whether they fall into the *Drosophila* or *Lymantria* categories have been recorded by Harrison and Doncaster (1914), Kuttner (1909), Banta (1916), de la Vaulx (1921), Sexton and Huxley (1921), and by Keilin and Nuttall (1919).

3. *Intersexuality in the mammal.*

(a) *Intersexuality due to abnormality in the time of the differentiation of the gonads.* Abnormality of the reproductive system taking the form of an intimate mixture of male and female structures belonging to the accessory sexual apparatus is not uncommon among the domesticated mammals, and many cases have also been recorded in the human subject. The typical history in these cases is that an individual, regarded as a female during the earlier part of its life, later assumes many of the characters of the male. This peculiar type of abnormality is particularly common in the goat and pig. In the goat cases are known in which an individual which actually won prizes when shown as an immature female, from the time of sexual maturity became more and more like the male: its beard grew, its head became male-like, and about it there hung the pungent smell so characteristic of the male. In its behavior it resembled the "rig," a male with maldescended testes, but its external genitalia retained the form of a vulva-like aperture with an over-

large clitoris. When the internal genitalia from such a case are examined there are found paired gonads lying in the situation of ovaries or somewhere along the track of the migrating testes, which on section show the structure typical of the maldescended testis; and an accessory sexual apparatus composed of more or less well defined epididymes, vasa deferentia, seminal vesicles, prostate, Cowper's glands, uterus, and vagina, the latter in some cases having failed to establish communication with the vulva.

The literature contains many references to this type of abnormality in the human, goat, and pig, but these were treated as isolated examples and no successful effort was made to give to them a common interpretation until Crew (1923) examined a considerable number of cases in the goat, pig, horse, cattle, sheep, and camel. In a few of the cases examined, the external genitalia had the form of an unremarkable vulva and clitoris; in others the rectile organ though female in form was unusually large and prominent; in others it was distinctly peniform yet imperfectly canaliculized. In a few instances there was a solid conical elevation on the abdominal wall where in the normal male the penis ends.

In all cases the differentiation of the Müllerian and Wolffian derivatives was imperfect, and the accessory sexual apparatus consisted of an intimate mixture of more or less well developed male and female structures. The most variable in its degree of development was the uterus.

It was found on examination that the cases of this condition in the pig fell cleanly into one of two classes, (1) those in which no morphological evidence of the previous or present existence of ovarian tissue could be found in the gonads which were entirely composed of testicu-

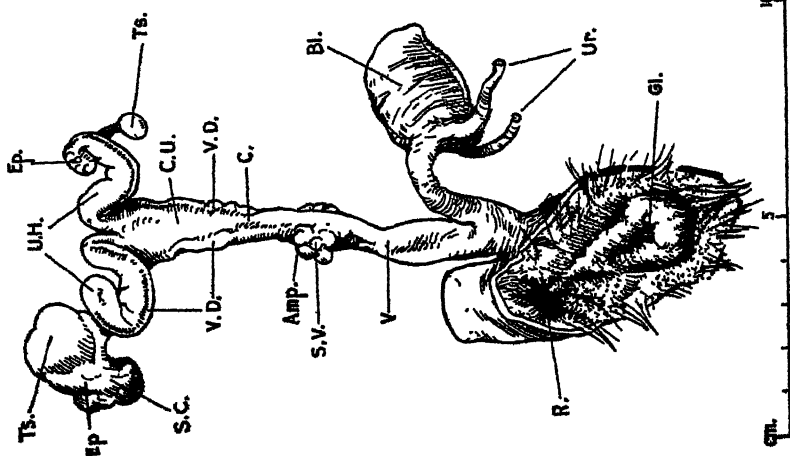


FIG. IIA

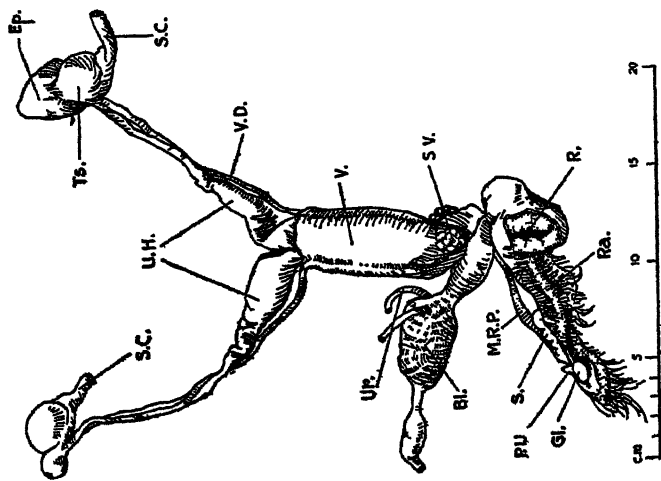


FIG. IIB

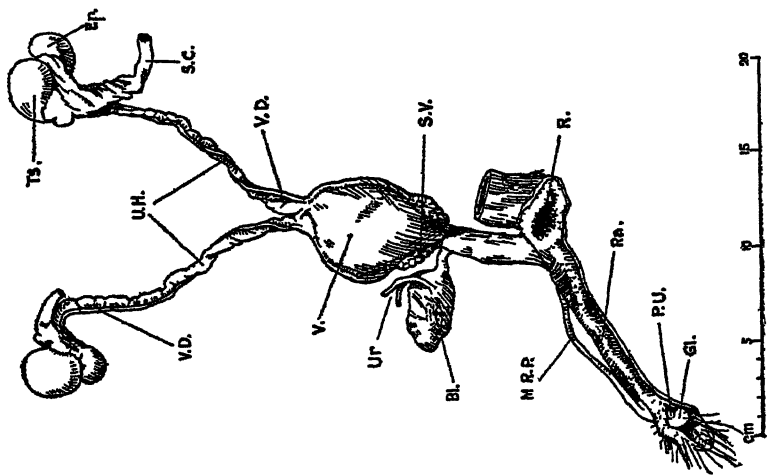


FIG. IIC

FIG. IIA, B, C. TYPES OF INTERSEXUALITY ENCOUNTERED IN THE GOAT

Amp., ampulla of vas deferens; *Bl.*, urinary bladder; *C.U.*, clitoris; *Ep.*, epididymis; *Gl.*, glands penis; *M.R.P.*, retractor penis; *P.U.*, process urethrae; *R.*, rectum; *Ra.*, median raphe of perineum; *S.*, flexures of corpus cavernosum penis; *S.C.*, seminal vesicle; *S.V.*, vas deferens; *U.H.*, uterine horns; *U.*, ureters; *V.*, vagina; *V.D.*, vas deferens; *Va.*, vulval cleft.

lar tissues with a histological structure varying with the position of the testis along the line between the primitive position and the scrotum, but always exhibiting some degree of degenerative change; and (2) those in which both ovarian and testicular tissues were present, the gonads being one an ovary, the other a testis; one an ovary, the other an ovotestis; or both being ovotestes. In one case there were paired ovaries within the abdominal cavity and paired testes beneath the skin of the perineum.

It was noted that in the cases of class 2 in which one gonad was an ovary, this gonad was always the left one, and that in an ovotestis the ovarian tissue was invariably cephalad to and sharply separated by a well defined belt of connective tissue from the caudad testicular portion. The ovarian tissue was invariably of apparently normal structure histologically, whereas in the testicular tissue the spermatogenic was always degenerate to some degree and the interstitial plentiful.

Those individuals in which the external genitalia were distinctly abnormal had been identified as "hermaphrodites" or "wilgils" by the breeders, and had been slaughtered while still immature. The few in which the external genitalia had the form of an unremarkable vulva and clitoris had been regarded as females until about the time of sexual maturity, when it was noted that instead of assuming the sexual characterization of the adult female they had begun to exhibit the secondary gonadic characters of the male type, and that the clitoris had begun to increase in size. The sexual behavior of such of these individuals as proved later to belong to class 1 was as that of the "rig," a male with maldescended testes. The behavior of such as belonged to class 2 was imperfectly male. They were

slaughtered because of their curious behavior and because they failed to breed.

The fact that in one class of these cases of reproductive abnormality there is no ovarian tissue and no suggestion that there ever had been any, whereas in the other class there is ovarian tissue of apparently normal structure, points to the conclusion that the two classes are different in their nature. If ovarian tissue had ever been present in the case of class 1, it should have persisted, since in those cases in which ovarian tissue is present it is invariably of normal structure. It is proposed to regard the two classes as being distinct and to treat them separately.

During ontogeny there is a period in which the differentiation of the sexual organization is timed to take place. At the beginning of this period which follows a preliminary phase of growth and organ formation, the reproductive system consists of (1) paired gonads of indifferent histological structure; (2) a rudimentary accessory sexual apparatus composed of Mullerian and Wolffian ducts; (3) external genitalia represented by the growing urogenital sinus and genital tubercle. From this initial type of reproductive architecture, possessed in common by all individuals, genotypic male and female alike, one or other type of differentiated sexual organization, male or female, is attained. The indifferent gonads become testes or else they become ovaries; if they become testes then the Wolffian ducts continue their development to become the functional deferent ducts of the testes, while the further development of the Müllerian ducts ceases and the external genitalia become scrotum and penis. If the indifferent gonads become ovaries the Müllerian ducts continue their development to become the functional uterus with cornua and Fallopian tubes and vagina, while the develop-

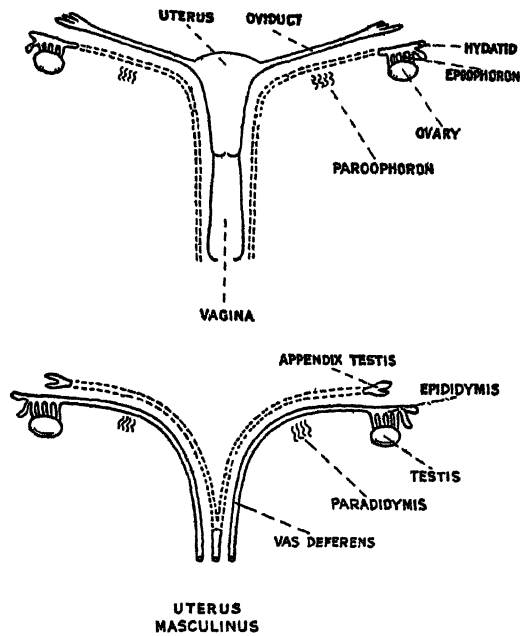


FIG. 12A

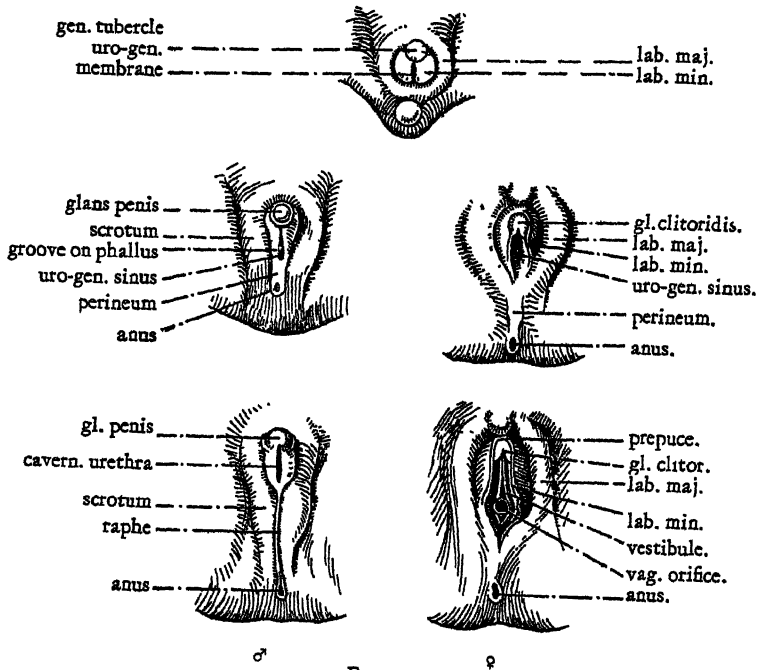


FIG. 12B

FIG. 12A, B. DIAGRAMS ILLUSTRATING THE ALTERNATIVE DEVELOPMENT OF THE INTERNAL AND EXTERNAL GENITALIA FROM A COMMON EMBRYONIC TYPE
A, the internal genitalia (after Broman); B, the external genitalia (after Hertwig)

ment of the Wolffian ducts ceases and the external genitalia assume the form of vulva and clitoris. Sexual differentiation is alternative and the end-product is an organization appropriate to the functional female or else to the functional male.

Between the differentiation of the various structures of the sex-equipment there is a time relation. The first structure to begin its differentiation is the gonad, the next, it is assumed, the external genitalia, and finally the structures of the accessory sexual apparatus. The results of gonadectomy and gonad implantation have shown perfectly clearly that for the appropriate differentiation of the rest of the sex-equipment the differentiated gonad is necessary. In the presence of functional testicular tissue the sexual organization appropriate to the functional male is assumed; in the presence of functional ovarian tissue that appropriate to the functional female. Such differentiation is pursued under the control of specific male and female sex-hormones elaborated by the testis and ovary respectively. Since the different structures of the sex-equipment respond to the physiological stimulus of the sex-hormones at different times during ontogeny it can be assumed that the threshold of response to this stimulus differs in different cases, and that before this threshold of response is reached a certain degree of undifferentiated growth is required. If the effect of the functioning of the differentiated testis is to inhibit the further development of the Müllerian ducts and their derivatives and to encourage the fuller development of the derivatives of the Wolffian ducts and to model the growing urogenital sinus and genital tubercle into scrotum and penis, then it is necessary only to explain the differentiation of the embryonic gonad into testicular tissues in order to explain

the complete assumption of a male type sexual organization by the individual.

This can be done if it is assumed that the gonad in its indifferent stage is ambivalent as regards its future mode of differentiation (though not completely so since its tissues are chromosomally either male or female, XO or XX), and that this differentiation is pursued under the direction of male-differentiating and female-differentiating substances elaborated by the male-determining and female-determining factors respectively. In the genotypic male (XO in sex-chromosome constitution) it is the rule for the male-differentiating substances to be effectively in excess over the female-differentiating substances during that period of development when the differentiation of the gonad is timed to take place, whereas in the genotypic female the female-differentiating substances are effectively in excess during this period.

These suggestions can be illustrated graphically as under classifications shown in figure 13.

The interpretations of the conditions found in class 1 can now be attempted. In these cases there were paired mal-descended testes, more or less well developed derivatives of both Müllerian and Wolffian ducts, external genitalia ranging from those of the apparently normal female to those of the grossly imperfect male. The cases could be readily arranged in a series according to the degree of imperfection of the external genitalia and of the degree of development of the Müllerian duct derivatives.

The fact that they could be so arranged suggests that they are one and all but grades of the same condition and that between them there exists a time relation. It must be stated clearly that there was no evidence which suggested that the abnormal individuals were free-mar-

tins (see Part II), cases of sex-reversal in a genetically determined female (see Part II), or cases of true "glandular hermaphroditism" in which the ovarian tissue had been removed at an earlier stage of development. They will be interpreted as instances of abnormal sexual differentiation in the genotypic male and the following assumptions will be made:

(1) The stimulus to differentiation of the remainder of the sex-equipment is, in the mammal, localized in the gonads.

(2) The abnormalities pertain only to the earlier stages of sexual development.

It is recognized that in this differentiation other agencies than the sex-hormone are involved, the other endocrines, for example, and that for effective differentiation there must be appropriate nutrition, but for the present these are disregarded.

For purely descriptive purposes it is assumed that in the process of the differentiation of the sex-organization in a genotypic male, excluding that of the gonads, there are three overlapping phases (1) the modelling of the external genitalia; (2) the atrophy of the Müllerian ducts; and (3) the further development of the

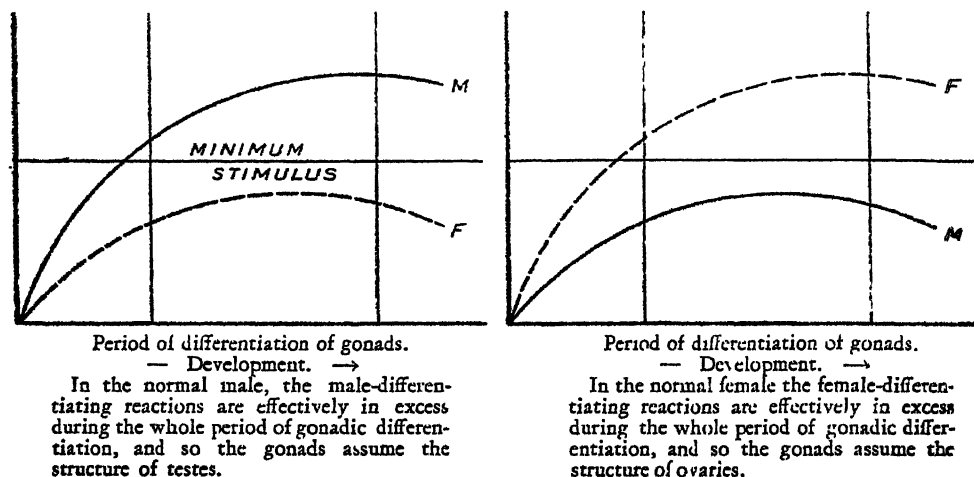


FIG. 13. DIFFERENTIATION OF GONADS

(3) The influence of the gonad in the mammal at this stage is such as inhibits the further development of these structures of the accessory sexual apparatus appropriate to the alternative functional sex, and that these structures, in the absence of such inhibition, would continue their development unchecked.

(4) There exists a different threshold of response to the sex-differentiating stimulus on the part of different structures of the sex-equipment and at different times during the development of one and the same structure.

Wolffian duct derivatives. For the sake of simplicity it is assumed that for all these structures there is one and the same minimum stimulus which, provided by the male sex-hormone elaborated by the testis, will evoke the specific response toward appropriate development. It is also assumed that when once the undirected development of any structure has proceeded for some time then that structure is no longer capable of responding to the stimulus if and when this is exhibited.

In *A*, the minimum stimulus necessary for proper differentiation is exhibited

before the time for differentiation has been reached, and as a consequence the differentiation is such that a completely male organization is established.

In *B*, in consequence of a retardation in the elaboration of the sex-hormone or of the production thereof at a slower rate, the differentiation of the external genitalia is partially undirected, and the result is grossly imperfect external genitalia in an otherwise normal male. The erectile organ will be most affected, for the

the Wolffian derivatives will not be so complete.

In *E*, the required stimulus is never exhibited during the period of the differentiation of the accessory sexual apparatus and external genitalia and the end-result will be the full grown embryonic form.

In the absence of the proper endocrine control during the period of differentiation of the accessory sexual apparatus and external genitalia, these structures pursue a parallel development under the common

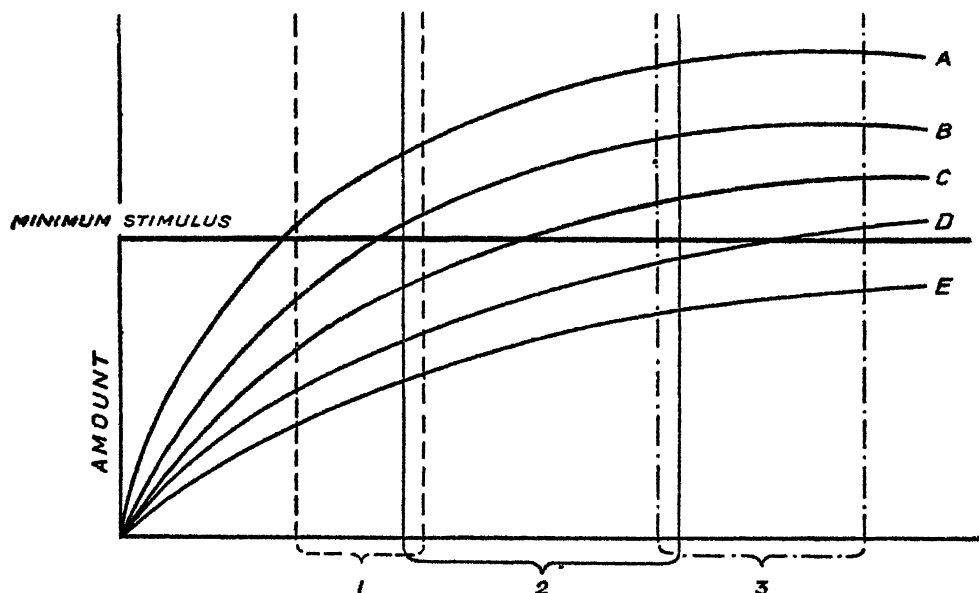


Fig. 14. SPECULATIVE INTERPRETATION OF THE DIFFERENT GRADES OF INTERSEXUALITY

scrotum of the normal male is sessile, and if in an abnormal male the testes descend through the inguinal canals they will become accommodated in a scrotum very much, if not quite, like that of the normal.

In *C*, in consequence of a greater retardation or still slower production, the end-results will be external genitalia even more imperfect and Müllerian duct derivatives further developed.

In *D*, the external genitalia will be as in *C*, the Müllerian derivatives will be better developed, whereas the development of

stimulus of nutrition. Epididymes, vasa deferentia, and seminal vesicles develop from the Wolffian duct, uterus and vagina from the Müllerian, and if such undirected growth continues, then after a time these structures will have lost their embryonic plasticity, and will fail to respond to the stimulus of the sex-hormone if and when this is exhibited later. The degree of development of the derivatives of the Müllerian ducts in a male and of the Wolffian ducts in a female and especially the degree of imperfection of the external

genitalia in a male, will provide significant indication as to the time during development at which the sex-hormone was exhibited.

These grades of abnormality of the reproductive system in the pig are thus to be explained as the result of the more or less complete absence, or of the qualitative or quantitative insufficiency, of the tissue in which the sex-hormone has its origin during that period of development when the differentiation of the rest of the sex-equipment occurs. But since this differentiation of the gonad occurs before the time of the assumption of many of the secondary gonadic characters, where will be exhibited then that time is reached. So it can happen that an individual whose external genitalia, really nothing more than a full grown urogenital sinus and genital tubercle, are indistinguishable from those of an immature female, may assume the secondary gonadic characters of the functional male and exhibit the exaggerated male sex instincts of a rig. It is possible that the testes of the male and the structures of the mechanism concerned in their descent pursue a parallel and corresponding development and differentiation up to the point when descent occurs, and that if the differentiation of the testis is retarded in any way, the proper association of testis and gubernacular apparatus is prevented or embarrassed so that the maldescent occurs.

The frequency of this type of abnormality in the pig, and the facts that it is more common in certain districts than in others, and that certain individuals in successive matings yield one or more of these intersexual offspring, point to the conclusion that this retardation or insufficiency of the sex-hormone is a character in the genetic sense.

In order to explain this retardation in the exhibition of the sex-hormone the

following assumption is made. Different male-determining and female-determining gene complexes elaborate their sex-differentiating substances at different rates or come into action at different times. The intersexual individual of this class is the result of the mating of individuals which transmit to their offspring that sex-determining gene complex in which the factors are "slowly-elaborating" in nature, so that the minimum stimulus for differentiation of the gonad in the male is not exhibited at the critical time during development.

It is stated that after complete ovariectomy the Müllerian duct derivatives undergo considerable atrophy. In the intersexual pig the uterus is often very well developed indeed and yet testicular tissues alone are present. It will be found that if testicular grafts are placed in an ovariectomized female the uterus will not undergo atrophy. The action of the sex-hormone of the male is to inhibit the further development of the growing Müllerian ducts; it does not effect an atrophy of the fully developed uterus, in fact it would seem that the adult structures of the accessory sexual apparatus do not atrophy when either ovary or testis is present.

(b) *Intersexuality due to abnormality in the mode of differentiation of the gonad.* The cases in class 2 are instances of as perfect intersexuality as is possible in the mammal. The essential feature of this condition is that both ovarian and testicular tissues shall be present synchronously or consecutively in one and the same individual. The mammal can and occasionally does possess both kinds of gonadic tissues, but it cannot function both as male and female since the external reproductive organs cannot be both male and female in their architecture. Moreover, oögenetic tissue cannot flourish in a scro-

tum nor spermatogenic within the abdominal cavity. Crew (1921) and Moore (1923) have shown that the optimum temperatures for efficient ovarian and spermatogenic functioning are widely different, and that the temperature within the abdominal cavity is considerably higher than that within the scrotum. Functional hermaphroditism is impossible, therefore, in the mammal.

The cases examined by Crew and those recorded in the literature are similar to those of class 1 in every respect save that the gonads include both ovarian and testicular tissue. To interpret these cases of "glandular hermaphroditism" it is necessary only to explain the presence of both kinds of gonadic tissues, since the abnormalities of the accessory sexual apparatus and of the external genitalia can be explained most simply and yet quite satisfactorily by assuming that they are exactly the same in nature and in origin as those found in the intersexual male of class 1. These intersexes are to be found among the herds that produce the intersexual individuals of class 1; in one and the same litter both kinds of abnormal offspring may be produced.

In the pig the relation of ovarian and testicular tissues is remarkable, as has already been pointed out. The cases in which two ovaries are found within an abdominal cavity and two testes within an imperfect scrotum are to be interpreted as the result of the separation by the gubernacular apparatus of ovotestes. If an ovotestis is thus divided along the line of the connective tissue which invariably separates ovarian from testicular two distinct gonads will be found on one and the same side of the body. If the testicular portion migrates to a situation beneath the skin of the perineum it might be expected that functional spermatozoa would be elaborated. But even were this

the case, the imperfection of the external genitalia would not permit the individual to function as a male.

One point of considerable interest emerges from the study of these cases. If testicular tissue is present in one gonad, testis or ovotestis, an epididymis and vas will be found associated with it, but if the other gonad is an ovary no epididymis and no vas will be found on this side. There is more than hormone stimulation involved: it would seem that some mechanical stimulus to the maintenance of the epididymis and vas is supplied by a testis but not by an ovary.

The abnormality of the gonads can be explained if it is assumed (1) that in these classes, males genetically, the sex-determining gene complex included quickly-elaborating female-determining genes and slowly-elaborating male-determining genes; and (2) that the differentiation of the gonads is not synchronous but consecutive, the left being affected before the right, and the cephalad pole before the caudad. If these individuals are genetic males then as a consequence of the balance between male- and female-determining factors established at the time of fertilization, sooner or later the male differentiating reactions will be in excess, but if the male determining genes are slowly-elaborating and the female-determining genes are quickly-elaborating then the situation will be such that the female-differentiating reactions will first exert the necessary minimum stimulus for gonadic differentiation and ovarian tissue will be laid down, and that shortly the male-differentiating reactions will overtake and replace the female, and the remainder of the differentiation will be pursued under their control, testicular tissues being laid down. The relative amounts of ovarian and testicular tissues will provide an estimate of the time during the period of go-

nadic differentiation when one kind of sex-differentiating reaction replaced the other.

As a result of the simultaneous presence of ovarian and testicular tissues both male and female sex-hormones will be elaborated. It is assumed that this determination of the gonads has been retarded and that before it occurs the accessory sexual apparatus and external genitalia have assumed more or less the full-grown embryonic form. But this differentiation occurs before the time of the assumption of the secondary gonadic characters, and the structures concerned with these will be exposed to the action of both kinds of sex-hormone. The results are as those obtained in the experimentally produced hermaphrodite, a characterization suggesting that certain structures respond preferentially to one sex-hormone, others to the other. The phallus invariably enlarges, while the sexual behavior is exaggeratedly male.

If, on the other hand, the differentiation of the gonads, though abnormal in its mode, is normal in time, occurring before the differentiation of the rest of the sex-equipment is timed to take place, the situation can arise in which, owing to the presence of both ovarian and testicular tissue both types of sex-hormone are available for the direction of this differentiation. The external genitalia, in these circumstances will be predominantly, if not entirely male, for the reason that the somatic tissues being XO in constitution, will respond preferentially to the stimulus of the male sex-hormone. The internal genitalia will be a mixture of more or less well developed derivatives of both Müllerian and Wolffian ducts.

Intersexuality can thus occur in two

forms in the genetic male, one being the result of an abnormality in time of differentiation of the gonads, and the other of abnormality in the mode and in the time of the differentiation of the gonads. That it should be the male that is prone to such abnormality is not surprising, for the balance in the sex-determining gene-complex is known to be less stable in the digametic (XO) than in the monogametic (XX) sex.

Of course, it may well be that these individuals are genetic females (in fact, further investigation is providing evidence which would seem to show that they are), that the differentiation of the gonads is in the order right to left, caudad pole to cephalad, and that the female-determining factors are the relatively slowly-elaborating. Baker (1925) is definitely of this opinion and has brought forward evidence which supports his view. However, it is thought fit to present the above highly speculative interpretation in order to draw the attention of other workers to the advantages of the pig as experimental material for use in this particular field of biological enquiry.

In the goat and also in the human being, judging from the descriptions of ovotestes given by different writers (e.g., Krediet, 1921) the course of gonadic differentiation is different from that which obtains in the pig, as is also the time relation in the differentiation of the structures of the accessory sexual apparatus and external genitalia. Nevertheless, with a few modifications the scheme suggested for the pig can be adapted for the interpretation of the conditions found in the human intersexual, and of the very many hermaphrodites in the mammals, fish, and amphibia.

LITERATURE LIST

Marked * contain a good bibliography

GENERAL

- *BELL, W. BLAIR. 1920. The Sex Complex. Ballière Tindall & Cox.
- *CREW, F. A. E. 1925. Animal Genetics. Oliver & Boyd.
- DONCASTER, L. 1914. The Determination of Sex. Cambridge University Press
- EDBACHER, S. and RÖHLER, H. 1925. Beiträge zur Kenntniss der Arginase. III. Argininsatz und Sexualität. Zeit. physiol. Chemie, v. 145, pp. 273-282.
- *ELLIS, HAVELOCK. 1914. Man and Woman. Walter Scott.
- GRODDE, P., and THOMSON, J. A. 1889. The Evolution of Sex. Walter Scott.
- *GOLDSCHMIDT, R. 1923. The Mechanism and Physiology of Sex Determination. Methuen.
- HARTMANN, M. 1925. Untersuchungen über relative Sexualität. Biol. Zentralb., v. 48, pp. 449-467.
- HIGNER, R. W. 1914. The Germ-Cell Cycle in Animals. Macmillan.
- *LIPSCHÜTZ, A. 1924. The Internal Secretion of the Sex Glands. Heffer.
- MANOILOV, E. O. 1922-23. Identification of sex in plants by chemical reaction. Bull. Appl. Bot. (Russian), v. 13, pp. 503-505.
- *MEISENHIMER, I. 1922. Geschlecht und Geschlechter im Tierreich. Fischer.
- *MORGAN, T. H. 1914. Heredity and Sex. Columbia University Press.
- *MORGAN, T. H., BRIDGES, C. B., and STURTEVANT, A. H. 1919. Contributions to the Genetics of *Drosophila melanogaster*. Carn. Inst. Publ., No. 278.
- *MORGAN, T. H., STURTEVANT, A. H., MULLER, H. J., and BRIDGES, C. B. 1923. The Mechanism of Mendelian Heredity. Henry Holt.
- *MORGAN, T. H., BRIDGES, C. B., and STURTEVANT, A. H. 1925. The Genetics of *Drosophila*. Bibliog. Geneti., v. 2.
- SCHWETZER, J. 1923. Polyploidie und Geschlechtsverteilung bei *Splachnum sphericum* Schwartz. Flora, v. 116, pp. 1-72.
- SEARER, C. 1924. On the oxygen consumption rate of parts of the chick embryo and fragments of the earthworm. Proc. Roy. Soc. B, v. 96, pp. 146-156.
- SHULL, G. H. 1914. Sex-limited inheritance in *Lychnis diotis* L. Zeit. induct. Abst., v. 12, pp. 265-302.

- WEITSTEIN, V. F. 1924. Morphologie und Physiologie des Formwechsels der Moose auf genetischer Grundlage. Zeit. induct. Abst., v. 33, pp. 1-236.

INVERTEBRATA

- ANCEL, P. 1902-03. Histogenèse et structure de la glande hermaphrodite d'*Helix pomatia*. Arch. d. biol., v. 19, pp. 389-652.
- ASHWORTH, J. H. 1913. On some pseudo-hermaphrodite examples of *Daphnia pulex*. Proc. Roy. Soc. Edinb., v. 23, pp. 307-316.
- BANTA, A. M. 1916. Sex-intergrades in a species of Crustacea. Anat. Rec., v. 11, pp. 505-506.
- BURESCH, F. 1912. Untersuchungen über die Zwitterdrüse der Pulmonaten. Arch. f. Zellf., v. 7, pp. 314-343.
- CUÉNOT, L. 1891. Études morphologiques sur les échinodermes. Arch. d. biol., v. 11.
- . 1898. L'hermaphroditisme protandrique d'*Asterina gibbosa* et ses variations suivant les localités. Zool. Anz., v. 21, pp. 273-279.
- . 1899. Sur la détermination du sexe chez les animaux. Bull. Sci. Franc. Belg., v. 32.
- DÉLAGE, Y. 1902. Quelques expériences et observations sur les Astéries. Arch. zool. exp. et gén., v. 10, pp. 237-240.
- FALCONER. 1910. Abnormality in Spiders. Naturalist, p. 229.
- HERLANT, M. 1918. Un cas d'hermaphroditisme complet et fonctionnel chez *Paracentrotus lividus*. Arch. zool. exp. et gén., v. 57, pp. 28-31.
- HILL, J. P. 1917. A gynandromorph specimen of the earwig. Proc. Zool. Soc. Lond. p. 213.
- HULL, J. E. 1918. Gynandry in Arachnida. Jour. Genet., v. 7, pp. 171-182.
- ISHIKAWA, C. 1891. On the formation of eggs in the testis of *Gebia major* de Haan. Zool. Anz., v. 14, pp. 70-72.
- KULCZEŃSKY. 1885. Potworek obojnakowy pajaka. Cracow.
- KUTTNER, O. 1909. Untersuchungen über Fortpflanzungsverhältnisse und Vererbung bei Cladoceren. Intern. Rev. d. ges. Hydrobiol. u. Hydrographie, v. 2.
- NEBESKI, O. 1880. Beitrag zur Kenntniss der Amphipoden der Adria. Arb. zool. Instit. Wien., v. 3, pp. 110-162.
- NICHOLS. 1734. Phil. Trans. (quoted by Morgan & Bridges).

- PRESENER, P. 1920. Variations et leur hérédité chez les mollusques. Mém. Acad. Roy. Belg., v. 5, pp. 1-826.
- PREZ, J. 1885. Des effects du parasitisme. Soc. Linn. Bordeaux, v. 12, pp. 21-60.
- SCHÖNEMUND, E. 1912. Zur Biologie und Morphologie einiger Perlarten. Zool. Jahrb., v. 34, pp. 1-56.
- SEXTON, E. W. and HUXLEY, J. S. 1911. Intersexes in *Gammarus chevreuxi* and related forms. Jour. Mar. Biol. Ass., v. 12, pp. 506-556.
- SMITH, G. 1910-1913. Studies in the experimental analysis of sex. I-IX. Q.J.M.S., vols. 54-58.
- WHITNEY, D. D. 1915. The production of males and females controlled by food conditions in the English *Hydatina senta*. Biol. Bull., v. 29, pp. 41-45.
- . 1916. The control of sex by food in five species of rotifers. Jour. Exp. Zool., v. 20, pp. 163-296.
- Insecta*
- BLUNK, H. and SPEYER, W. 1924. Kopftausch und Heilungsvermögen bei Insekten. Zeit. wiss. Zool., v. 123, pp. 156-208.
- BOVERI, T. 1915. Über die Entstehung der Eugsterischen Zwitterbienen. Arch. f. Entw., v. 41, pp. 264-311.
- BRIDGES, C. B. 1917. Deficiency. Genet., v. 2, pp. 445-465.
- . 1919. Vermilion deficiency. Jour. gen. Physiol., v. 1, pp. 645-656.
- . 1916. Non-disjunction as a proof of the chromosome theory of heredity. Genet., v. 1, pp. 1-52, 107-163.
- . 1921. Triploid intersexes in *Drosophila melanogaster*. Sci., v. 54, pp. 252-254.
- . 1921. Genetical and cytological proof of non-disjunction of the IV chromosome of *Drosophila melanogaster*. Proc. Nat. Acad. Sci., v. 7, pp. 186-192.
- . 1925. Sex in relation to chromosomes and genes. Amer. Nat., v. 59, pp. 127-137.
- . 1925. Haploidy in *Drosophila melanogaster*. Proc. Nat. Acad. Sci., v. 11, pp. 706-710.
- COCKAYNE, E. A. 1915. Gynandromorphism and kindred problems. Jour. Genet., v. 5, pp. 75-131.
- ENGELHARDT, v. 1914. Über den Bau der gynandromorphen Bienen. Zeit. wiss. Insektenb.
- FINKLER, W. 1923. Kopftransplantationen an Insekten. Arch. mikr. Anat., v. 99, pp. 104-133.
- GOLDSCHMIDT, R. 1925. Über die Erzeugung der höheren Stufen der männlichen Intersexualität bei *Lymantria dispar*. Biol. Zentralb., v. 45, pp. 134-136.
- , and others. 1920. Untersuchungen über Intersexualität. Zeit. induct. Abst., v. 23, pp. 1-199.
- , and SAGUSCHI. 1922. Die Umwandlung des Eierstocks in einen Hoden beim intersexuellen Schwammspinner. Zeit. Anat. Entw., v. 65, pp. 226-254.
- , and PARISER, K. 1923. Triploide Intersexe bei Schmetterlingen. Biol. Zentralb., v. 43, v. 43, pp. 446-452.
- HARRISON, J. W. H. 1919. Studies on the hybrid Bistoninae. IV. Concerning the sex ratio and related problems. Jour. Genet., v. 9, pp. 1-38.
- , and DONCASTER, L. 1914. On hybrids between moths of the geometric subfamily Bistoninae. Ibid., v. 3, pp. 229-248.
- HEYMONS, R. 1890. Über die hermaphrodite Anlage der Sexualdrüsen beim Männchen von *Phyllodromia germanica*. Zool. Anz., v. 13, pp. 451-457.
- HUETTNER, A. 1922. The origin of the germ-cells in *Drosophila melanogaster*. Jour. Morph., v. 37, pp. 385-424.
- KRILIN, D. and NUTTALL, G. H. F. 1919. Hermaphroditism and other abnormalities in *Pediculus humanus*. Parasit., v. 11, pp. 279-288.
- KELLOGG, V. L. 1904. Influence of the primary reproductive organs on the secondary sexual characters. Jour. Exp. Zool., v. 1, p. 601.
- KOPRĆ, S. 1911. Untersuchungen über Kastration und Transplantation bei Schmetterlingen. Arch. f. Entw., v. 33, pp. 1-116.
- . 1922. Physiological self-differentiation of the wing-germs grafted on caterpillars of the opposite sex. Jour. Exp. Zool., v. 36, pp. 469-475.
- MEHLING, E. 1915. Über die gynandromorphen Bienen des Eugsterischen Stockes. Verh. phys.-med. Ges. Würzb.
- MEISENHÖRMER, J. 1909. Experimentelle Studien zur Soma und Geschlechtsdifferenzierung. Jena.
- METZ, C. W. 1920. Observations on the sterility of mutant hybrids in *Drosophila virilis*. Proc. Nat. Acad. Sci., v. 6, pp. 421-423.
- MOHR, O. L. 1919. Character changes caused by mutation of an entire region of a chromosome in *Drosophila*. Genet., v. 4, pp. 275-282.
- . 1923. A genetical and cytological analysis of a section deficiency involving four units of the X-chromosome in *Drosophila melanogaster*. Zeit. induct. Abst., v. 32, pp. 108-232.

- MORGAN, L. V. 1925. Polyploidy in *Drosophila melanogaster* with two attached X-chromosomes. Genet., v. 10, pp. 148-178.
- *MORGAN, T. H. and BRIDGES, C. B. 1919. The Origin of Gynandromorphs. Carn. Inst. Publ., No. 278, pp. 1-122.
- MULLER, H. J. and DUFFEL, A. L. 1926. Chromosome breakage by X-rays and the production of eggs from genetically male tissue in *Drosophila*. Brit. Jour. Exp. Biol., v. 3, pp. 85-122.
- NACHTSHEIM, H. 1913. Cytologische Studien über die Geschlechtsbestimmung bei der Honigbiene. Arch. f. Zellf., v. 11, pp. 169-241.
- . 1923. Parthenogenese, Gynandromorphismus und Geschlechtsbestimmung bei Phasiden. Zeit. indukt. Abst., v. 30, pp. 287-289.
- NEWELL, W. 1914. Inheritance in the honey bee. Sci., v. 41, pp. 218-219.
- OUDEMANS, J. TH. 1899. Falter aus kastrierten Raupen, wie sie aussehen und wie sie sich benehmen. Zool. Jahrb., v. 12, pp. 71-88.
- PREEL, H. 1915. Über die Beziehung zwischen primären und sekundären Sexualcharakteren bei Schmetterlingen. Zool. Jahrb., v. 33, pp. 183-224, 593-597.
- SANDHOUSE, G. A. 1923. A gynandromorphic bee of the genus *Osmia*. Amer. Nat., v. 57, pp. 569-570.
- SCHRAEDER, F. and STURTEVANT, A. H. 1923. A note on the theory of sex-determination. Amer. Nat., v. 57, pp. 379-381.
- SIEBOLD, C. TH. 1866. Ersatz der abgestorbenen Zwittermutter der Eugsterschen Zwitterstocks in Constanx. Bienenzeit.
- STANDFUSS, B. M. 1896. Handbuch der paläarktischen Grossschmetterlinge. Jena.
- STURTEVANT, A. H. 1920. Genetic studies on *Drosophila simulans*. I. Hybrids with *Drosophila melanogaster*. Genet., v. 5, pp. 488-500.
- . 1920. Intersexes in *D. simulans*. Sci., v. 51, pp. 379-380.
- . 1920. The Vermilion gene and gynandromorphism. Proc. Soc. Exp. Biol. Med., v. 17, pp. 70-71.
- . 1921. Genetic studies on *D. simulans*. II. Sex-linked group of genes. III. Autosomal genes. General discussion. Genet., v. 6, pp. 43-64, 179-207.
- TOYAMA, K. 1906. Studies on the hybridology of insects. I. On some silkworm crosses with special reference to Mendel's Law of Heredity. Bull. Coll. Agric., Tokyo, v. 7, pp. 262-393.
- WENKE, K. 1906. Anatomie eines *Argyminis paphia* Zwitter. Zeit. wiss. Zool., v. 84, pp. 95-138.
- WHEELER, E. W. 1910. A Gynandromorphous mutilid *Pseudomethoca canadensis*. Psyche, v. 17, pp. 186-189.

VERTEBRATA

- SCHREINER, K. E. 1904. Über das Generationsorgan von *Myxine glutinosa* L. Biol. Zentralb., v. 24, pp. 91-104, 121-128, 162-173.

Pisces

- AIDA, Y. 1921. On the inheritance of colour in a fresh-water fish, *Aploccheilus latipes*, with special reference to sex-linked inheritance. Genet., v. 6, pp. 554-573.
- GRASSI, B. 1919. Nuove ricerche su la storia naturale dell'Anguilla. R. Com. talassograf, Ital., Mem. 47.
- WINGE, O. 1922. A peculiar mode of inheritance and its cytological explanation. Jour. Genet., v. 12, pp. 137-144.
- . 1923. Crossing-over between the X- and the Y-chromosome in *Lebistes*. Ibid., v. 13, pp. 201-207.

N.B. A complete list of cases of hermaphroditism in fish will be found in Bashford Dean's "Bibliography of Fish."

Amphibia

- HARMS, W. 1914. Experimentelle Untersuchungen über die innere Sekretion der Keimdrüsen. Jena.
- HERTWIG, R. 1912. Über den derzeitigen Stand des Sexualproblems. Biol. Zentral, v. 32, pp. 66-129.
- KUSHAKEVITCH, S. 1910. Die Entwicklungsgeschichte der Keimdrüsen von *Rana esculenta*. Festschr. f. R. Hertwig, v. 2.
- PFLÜGER, W. 1882. Über die geschlechtsbestimmende Ursachen und die Geschlechtsverhältnisse der Frösche. Pflüg. Arch., v. 29, pp. 13-40.
- SCHMIDT-MARCHEL, W. 1908. Über Pseudo-Hermaphroditismus bei *Rana esculenta*. Arch. mikr. Anat., v. 72, pp. 516-539.
- SWINGLE, W. W. 1925. Sex-differentiation in the bullfrog. Amer. Nat., v. 59, pp. 154-176.
- WITSCH, E. 1914. Die Keimdrüsen von *Rana temporaria*. Arch. mikr. Anat., v. 85, pp. 9-113.
- . 1915. Studien über die Geschlechtsbestimmung bei Fröschen. Ibid., v. 86, pp. 1-50.

Homo

- BULLOCK, W. and SEQUEIRA, J. H. 1905. Relation of adrenals to the sexual organs. *Trans. Path. Soc. Lond.*, v. 56, pp. 189-208.
- GLYNN, E. E. 1911-12. The adrenal cortex, its tests, tumours, its relation to other ductless glands and especially to sex. *Quart. Jour. Med.*, v. 5, pp. 158-192.
- GRÄFENBERG, E. 1922. Die Geschlechtsspezifität des weiblichen Blutes. *Arch. f. Gynäk.*, v. 117, pp. 52-53.

Aves

- BERNER, O. 1923. Virilisme surrénal chez une poule. *Rev. franc. d'endocr.*, v. 1, pp. 474-492.
- BOND, C. J. 1913. Some points of genetic interest in regeneration of the testis after experimental orchiectomy in birds. *Jour. Genet.*, v. 3, pp. 131-139.
- . 1913. On a case of unilateral development of secondary male characters in a pheasant, with remarks on the influence of hormones in the production of secondary sexual characters. *Ibid.*, pp. 205-217.
- *CREW, F. A. E. 1923. Studies in intersexuality. II. Sex-reversal in the fowl. *Proc. Roy. Soc., B*, v. 95, pp. 256-278.
- . 1923. The Cocky-feathered hen. *Nat. Poult. Jour.*, pp. 579-580.
- MACKLIN, M. 1923. Description of material from a gynandromorph fowl. *Jour. Exp. Zool.*, v. 38, pp. 355-375.
- POLL, H. 1909. Zur Lehre von sekundären Sexualcharakteren. *Sitzb. Ges. naturf. Freunde, Berlin*, v. 6, pp. 331-358.
- RIDDLE, O. 1925. Birds without gonads. *Brit. Jour. Exp. Biol.*, v. 2, pp. 211-248.
- . 1925. On the sexuality of the right ovary of birds. *Anat. Rec.*, v. 30, pp. 365-382.
- SEREBROVSKY, A. S. 1925. Somatic segregation in domestic fowl. *Jour. Genet.*, v. 16, pp. 33-42.
- WEBER, M. 1890. Über einen Fall von Hermaphroditismus bei *Fringilla caelebs*. *Zool. Anz.*, v. 13, pp. 508-512.
- BAKER, J. R. 1925. On the descended testes of sex-intergrade pigs. *Q.J.M.S.*, v. 69, pp. 689-701.
- CREW, F. A. E. 1921. The cause of the aspermatic condition of the imperfectly descended testis. Thesis, Edinburgh.
- . 1923. Studies in intersexuality I. A peculiar type of developmental intersexuality in the male of the domesticated mammals. *Proc. Roy. Soc., B*, v. 95, pp. 90-109.
- KREDIET, G. 1921. Ovariectomie bei der Ziege. *Biol. Zentralb.*, v. 47, pp. 447-455.
- LIPSCHUTZ, A., and KRAUSE, W. 1923. Temps de latence dans l'hermaphroditisme expérimental. *Ibid.*, pp. 1135-1137.
- MALONE, J. Y. Spermatogenesis in the dog. *Trans. Amer. Micro. Soc.*, v. 37, pp. 97-110.
- MOORE, C. R. 1921. III. Artificial hermaphroditism in rats. *Ibid.*, v. 33, pp. 129-171.
- . 1921. IV. Gonad transplantation in the guinea-pig. *Ibid.*, pp. 365-389.
- , and QUICK, W. J. 1923. The scrotum as a temperature regulator for the testis. *Amer. Jour. Physiol.*, v. 68, pp. 70-79.
- PAINTER, T. S. 1921. The Y-chromosome in mammals. *Sci.*, v. 53, pp. 503-504.
- . 1922. Studies in mammalian spermatogenesis. I. The spermatogenesis of the opossum. *Jour. Exp. Zool.*, v. 35, pp. 13-46.
- . 1923. The Spermatogenesis of man. *Ibid.*, v. 37, pp. 291-321.
- . 1924. III. The fate of the chromatin-nucleolus in the opossum. *Ibid.*, v. 39, pp. 197-228.
- . 1924. IV. The sex chromosomes of monkeys. *Ibid.*, pp. 433-451.
- . 1924. V. The chromosomes of the horse. *Ibid.*, pp. 229-248.
- PARKES, A. S. 1923. Head-length dimorphism of mammalian spermatozoa. *Q.J.M.S.*, v. 67, pp. 617-625.
- SAND, K. 1921. Études expérimentales sur les glandes sexuelles chez les mammifères I. II. III. *Jour. physiol. path. gén.*, v. 19, pp. 305-322, 494-527.
- . 1923. L'hermaphroditisme expérimental. *Ibid.*, v. 20, pp. 472-487.
- STEINACH, E. 1912. Willkürliche Umwandlung von Säugetiermännchen in Tiere mit ausgeprägt weiblichen Geschlechtscharakteren und weiblicher Psyche. *Pflüg. Arch.*, v. 144, pp. 71-108.
- STEVENS, N. M. 1911. Heterochromosomes in the guinea-pig. *Biol. Bull.*, v. 21, pp. 155-167.
- VAULX, DE LA, R. 1921. L'intersexualité chez un crustacé cladocère (*Daphnia atkinsoni*). *Bull. Biol. Fran. Belg.*, v. 55, pp. 1-86.

Mammalia

- ALLEN, EZRA. 1918. Studies on cell division in the albino rat. III. Spermatogenesis. *Jour. Morph.*, v. 31, pp. 133-186.
- BACHHUBER, L. J. 1916. The behavior of the accessory chromosomes and of the chromatid body in the spermatogenesis of the rabbit. *Biol. Bull.*, v. 30, pp. 294-310.

- WINTWARTER, v. H., and SAINTMONT, G. 1909. Nouvelles recherches sur l'ovogénèse et l'organogénèse de l'ovaire des mammifères. VI Ovogénèse de la zone corticale primitive. Arch. d. biol., v. 24, pp. 165-267.
- WODSDALEK, J. E. 1913. Accessory chromosomes in the pig. Sci., v. 38, pp. 30-31.
- . 1913. Spermatogenesis in the Pig. Biol. Bull., v. 25, pp. 8-46.
- . 1914. Spermatogenesis in the horse. Ibid., v. 27, pp. 295-304.
- WODSDALEK, J. E. 1916. Causes of sterility in the mule. Ibid., v. 30, pp. 1-56.
- . 1920. Studies on the cells of cattle, with special reference to spermatogenesis and sex-determination. Ibid., v. 38, pp. 290-316.
- YOCUM, H.B. 1915-17. Some phases of spermatogenesis in the mouse. Univ. Calif. Publ., v. 16, pp. 371-380.
- ZELENT, C. and FAUST, E. C. 1915. Size-dimorphism in the spermatozoa from single testes. Jour. Exp. Zool., v. 18, pp. 187-240.





HUMAN TYPES

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THIS paper on human types embodies the results and records obtained by the author during investigations in America, Europe, Japan and the Philippines, and a discussion of the relation of this work to the general literature on the subject. More than 100,000 records have been tabulated by the writer. The persons measured or examined included 16,345 American Whites, 7,507 American Negroes, 5,298 Filipinos, 3,940 Japanese, 562 Chinese, 561 Spanish, 71 East Indians, and a few American Indians.

The problem of human types is one that has baffled the ages, and it is not yet in a fair way to complete solution. Many factors such as heredity, environment, isolation, dispersal, differentiation, crossing and recrossing have resulted in mosaics of peoples throughout the world. It would take too much space to try to unravel the complexities, but a word as to some of the chief transformations up to the present time may not be out of place.

The Neanderthal man of the Mousterian period in Europe was of the extreme Mesomorph, or intermediate form of man from the anatomical or morphological standpoint. Modifications of this form exist throughout Oceania and in Africa, and may be seen in Europe, as recorded in recent anthropological surveys in the small islands of Denmark (64). Throughout the Pacific area this form has been called Australoid, and in Africa occurs among the purer Negroes. It has

become modified among the Yellow-Brown peoples in Asia and America where it resembles the late Paleolithic forms of Europe. The modifications of the Neanderthal may be seen in Europe in the Spy skeletons, again at Krapina, and in Moravia and Bohemia, as well as in the Aurignacian and Solutrean forms, and the later Brno, Brûx, Combe Capelle and Cro-Magnon forms (70). As the people spread to the Mediterranean and Baltic basins, with the development of the harpoon and the use of fish as food, they became smaller and slenderer so that the type changed from that of the Mesomorph to that of the Hypermorph. The pigmentation increased in the Mediterranean basin and decreased in the Baltic. Fleure (32) has traced the changing types through southern Britain, Wales and Ireland, where the face grew narrower and longer and the orbits high and narrow instead of low and broad. Around the littoral of Europe somewhat inland, and in Scandinavia, the stature remained tall whereas it became small in the south. The peoples of the interior of Europe remained more of the Mesomorph type, broad and stocky.

Certain stocks that became isolated and lived under adverse conditions were reduced to a more or less infantile form, with short arms and legs and round heads and faces. This finds its extreme manifestation among the Negrillos of Africa, the Negritos of the Pacific, and the Malays, and in a more or less modified form among the peoples of the sub-arctic

regions, as the Siberians and Lapps. This type I have called the Hypomorph.

The three types, Hypermorph or high form, Mesomorph or medium form and Hypomorph or low form, are the three outstanding generalized forms of man. Only the first two are found in Europe or among the White peoples, whereas all three types are found among the Blacks and Yellow-Browns.

The chief anthropometric characters of the three types may be given in a general way as in table 1.

It may be seen that this method of classification of man into types cuts

are found together among men throughout the world.

The question arises as to whether the coördinate characters are the result of phylogeny or ontogeny; whether they are the result of evolution or of individual development. Evidence of the incoördinate conditions in evolution has been advanced by Hooten in a study of many characters of man and apes, conditions that he groups under the term asymmetrical evolution, but that might more properly be called incoördinate evolution. I called attention to similar conditions noted in the living in a pre-

TABLE 1
Generalized characters of the three types

CHARACTER	HYPOMORPH	MESOMORPH	HYPERMORPH
Stature.....	Small	Medium	Tall
Sitting height.....	High	Medium	Low
Legs.....	Short, broad	Medium	Long, narrow
Arms.....	Short, broad	Medium	Long, narrow
Body.....	Round	Bulky	Wiry
Neck.....	Broad	Medium	Narrow
Shoulders.....	Broad	Medium	Narrow
Thorax.....	Broad	Medium	Narrow
Hips.....	Broad	Medium	Narrow
Nose.....	Short, broad	Medium	Long, narrow
Ears.....	Short, broad	Medium	Long, narrow
Hands and feet.....	Short, broad	Medium	Long, narrow

squarely across the recognized races or groups of man, whether we take the grouping of Haddon (39) into Straight-Haired, Wavy-Haired and Woolly-Haired, or that of Hrdlička into White, Black and Yellow-Brown or almost any other classification of man that has been devised by anthropologists. The present classification into Hypomorph, Mesomorph and Hypermorph has the advantage of a large number of conformable characters, only the chief of which were grouped in table 1. It does not attempt to group into races, but only calls attention to some coördinate characters that

vious paper (19), where the suggestion was made that characters as well as types have undergone evolution and have become exaggerated in one direction or another. Thus the nose is broad and flattened in the Black, narrow and high in the White and intermediate in the Yellow-Brown. The woolly hair of the Black and the straight hair of the Yellow-Brown are extremes, neither of which has been reached in the White. The dark skin of the Black and the light skin of the White are more extreme than the intermediate coloring of the Yellow-Brown. The glabrous Yellow-Brown

and the hirsute White are more extreme than the intermediate hairiness of the Black. The ear type of the White is between that of the Black and of the Yellow-Brown. The large brain of the White and the small brain of the Black are more extreme than the brain of the Yellow-Brown. Similarly we might point out that the legs of the Negro are the longest and those of the Yellow-Brown the shortest, with the White in between; the arms, hands, feet, trunk, and many other parts of the body may be differentiated in like manner. These variables are but an illustration of oscillation in evolution which produces different results upon various characters under different conditions.

The result is that neither the White, nor the Black nor the Yellow-Brown is extreme nor is any one of them intermediate, in all of the characters mentioned. Continental areas have not produced homogeneous results. The White of Europe, the Black of Africa and the Yellow-Brown of Asia are not uniform in their characters in relation to each other. On the other hand the Hypomorph, Mesomorph and Hypermorph are uniform regardless of race or continental area. Other factors have been more potent than these in their formation. The Hypermorph has been found more extreme in its characters near the sea, as about the Mediterranean and Baltic and in Britain and Japan; the Mesomorph has remained more marked in character in the interior of continental areas; and the Hypomorph has been most extremely developed in the tropics and arctic regions under adverse living conditions.

The distribution of these types has been treated at some length in papers that have appeared during the past three years in the *American Journal of Anatomy*, (17), (18), (19). Their characters have

also been presented in a general way with descriptions of their movements, and of their development and evolution. The types will now be illustrated, and their exact measurements as found in typical persons will be given, with some discussion in detail as to the composition of the types. First, outline drawings will be given of the types among the Blacks and Yellow-Browns; then photographs will be used for the Whites. The outline drawings were made by projection from actual photographs, and in order to show the characteristic differences few lines were made. The outlines bring out the desired characters better than photographs, and the differences are more easily and clearly seen because no distracting or extraneous structures are shown.

1. TYPES OF THE BLACK RACE

Figures 1, 2 and 3 represent three American Negroes in side view and figures 4, 5 and 6 three Negritos of the Philippines in front view. Figures 1 and 4 are Hypomorph, figures 2 and 5 are Mesomorph, and figures 3 and 6 are Hypermorph.

The Hypomorph (17) has a broad, flattened nose that is button like, as in the infant, depressed at the root and along the bridge and over the ridge; eyes that are wide apart and nearly closed, with a tendency toward the Mongolian Fold; and thick, everted lips. The ears are small, rounded and semi-bowl shaped. The face and cranium are rounded and somewhat flattened in front.

The Mesomorph (17) has a broad, pyramidal nose, that is somewhat flattened but is not so much depressed as that of the Hypomorph at the root and along the bridge and over the ridge; eyes that are not so far apart, with a slight tendency toward the Mongolian

Fold; and a large mouth without the thick everted lips. The ears are large and not so bowl-shaped as in the Hypomorph, and the cranium and face are large and oval, without so much flattening in front.

Figures 7, 8 and 9 illustrate the proportions of the extremities in relation to the remainder of the body. Figure 7 is the Hypermorph, figure 8 the Mesomorph and figure 9 the Hypomorph. These are photographs of three Negritos of the

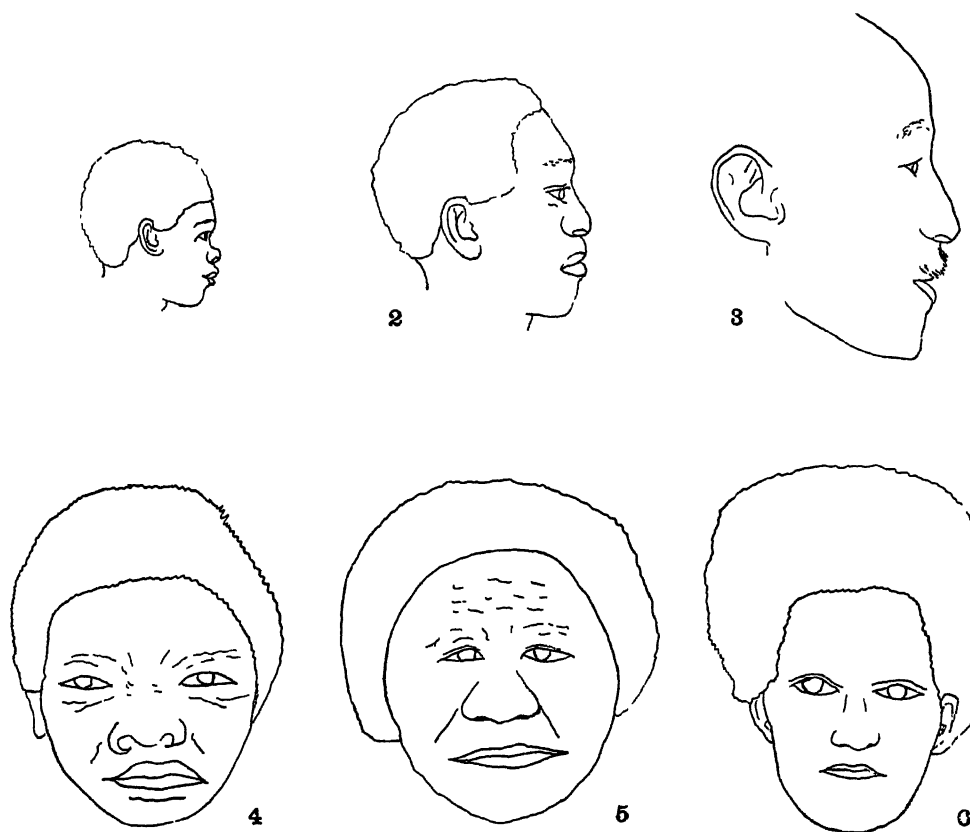


FIG. 1. AN AMERICAN NEGRO OF THE HYPOMORPH TYPE. FIG. 2. AN AMERICAN NEGRO OF THE MESOMORPH TYPE. FIG. 3. AN AMERICAN NEGRO MIXED WITH WHITE OF THE HYPERMORPH TYPE. FIG. 4. A FILIPINO NEGRO OF THE HYPOMORPH TYPE. FIG. 5. A FILIPINO NEGRO OF THE MESOMORPH TYPE. FIG. 6. A FILIPINO NEGRO OF THE HYPERMORPH TYPE.

The Hypermorph (17) has a narrow, long, high nose; eyes that are close together and wide open; a small mouth with thin lips; and thin ears with slender helix and everted tragus and antitragus. The cranium and face are long and narrow.

Philippines. The legs of the Hypomorph are relatively to stature or to sitting height very short, and the trunk is very long. The arms are also relatively short but not so much so as the legs. The hands and fingers are broad and short, and other characters of the Hypo-

morph may be seen. The legs of the Hypermorph are relatively to stature or to sitting height very long, and the trunk is very short. The arms are rela-

morph is in between the Hypomorph and Hypermorph.

The Black Hypermorph seems to be the result of mixture with some other



FIG. 7. A FILIPINO NEGRITO OF THE HYPERMORPH TYPE. FIG. 8. A FILIPINO NEGRITO OF THE MESOMORPH TYPE. FIG. 9. A FILIPINO NEGRITO OF THE HYPOMORPH TYPE

tively long but not so much so as the legs. The hands and fingers are long and narrow and other characters of the Hypermorph may be seen. The Meso-

stock; the typical ones are invariably of mixed stock in America, and probably also in Africa, therefore they may be left out in presenting the measurements of

typical persons of the Black Race. Measurements of a typical male and female Hypomorph and Mesomorph of the Black Race are given in table 2.

TABLE 2.
Actual measurements of typical Hypomorph and Mesomorph persons of the Black Race

	HYPOMORPH		MESOMORPH	
	Male	Female	Male	Female
Character:				
Stature	151 0	145 0	167 1	156 8
Sitting height	81 5	77 1	84 2	79 0
Leg length	69 7	67 9	82 9	77 8
Arm length	71 2	67 2	76 0	70 5
Acromion height	121 0	116 7	136 0	128 0
Head length	18 0	17 8	18 8	17 8
Head breadth	14 8	14 3	14 1	13 8
Nose length	4 3	4 2	4 65	4 0
Nose breadth	4 5	4 3	4 8	3 7
Ear length	5 4	5 2	5 9	5 5
Ear breadth	3 6	3 1	3 7	3 3
Index:				
<u>Sitting height</u> <u>Stature</u>	54 0	53 2	50 4	50 5
<u>Sitting height</u> <u>Leg length</u>	117 0	113 5	102 0	101 0
<u>Sitting height</u> <u>Arm length</u>	114 5	114 5	111 0	112 0
<u>Head breadth</u> <u>Head length</u>	82 0	80 0	75 0	79 0
<u>Nose breadth</u> <u>Nose length</u>	105 0	105 0	103 0	93 6
<u>Ear breadth</u> <u>Ear length</u>	66 5	59 8	63 0	60 0

The measurements and indices speak for themselves and show the obvious differences between the Hypomorph and Mesomorph. The stature of the Hypomorph is less than that of the Mesomorph, and as the sitting height of the two is not greatly different, the chief difference is in the leg length. The arm length shows less difference than the sitting height and much less difference

than the leg length. This comes out clearly in the indices. The sitting height divided by the stature shows a difference of about 5 per cent between the Hypomorph and the Mesomorph; the sitting height divided by the leg length shows a difference of about 12 per cent; and the sitting height divided by the arm length shows a difference of about 3 per cent. The index, of the sitting height divided by the stature, of the Mesomorph is a true Negro index whereas that of the Hypomorph is a Negrillo index. The same may be said of the cephalic index, or the head breadth divided by the head length, and of the nasal index, or the nose breadth divided by the nose length. This means that the True Negro is a Mesomorph and the Negrillo is a Hypomorph.

A great many other characters might be selected that would show as well as these the differences between the Hypomorph and Mesomorph but these will suffice. It must not be assumed that each person among the Blacks will be exactly like the examples given because this is not the truth. There are so many variants that only the extreme forms may be readily allocated to one group or the other. The great mass of the Blacks, in fact, will be found to be different from either the Hypomorph or the Mesomorph because these are the extremes. It may be possible to show that each person is like a Hypomorph or like a Mesomorph although not strictly one or the other. This will be brought out later in dealing with the Whites where a more intricate and detailed analysis of the types becomes possible. The Whites are more heterogeneous because of greater mixtures yet they have less distant extremes because of more homogeneous environment.

We may now turn to a consideration of the types of the Yellow-Browns.

II TYPES OF THE YELLOW BROWN RACE

The Blacks and the Yellow Browns have come together in India and Oceania as well as in southeastern Asia, therefore the Malays, Melanians and Polynesians should be treated as mixtures of those two races with the addition of some

Figure 10 shows a Hypomorph Filipino Negrito, figure 11, a Mesomorph Melanesian, figure 12, a Hypermorph Polynesian, figure 13, a Hypomorph Chinese, figure 14 a Mesomorph Chinese, and figure 15 a Hypermorph Japanese. These do not represent the only types of the groups to which they belong, but

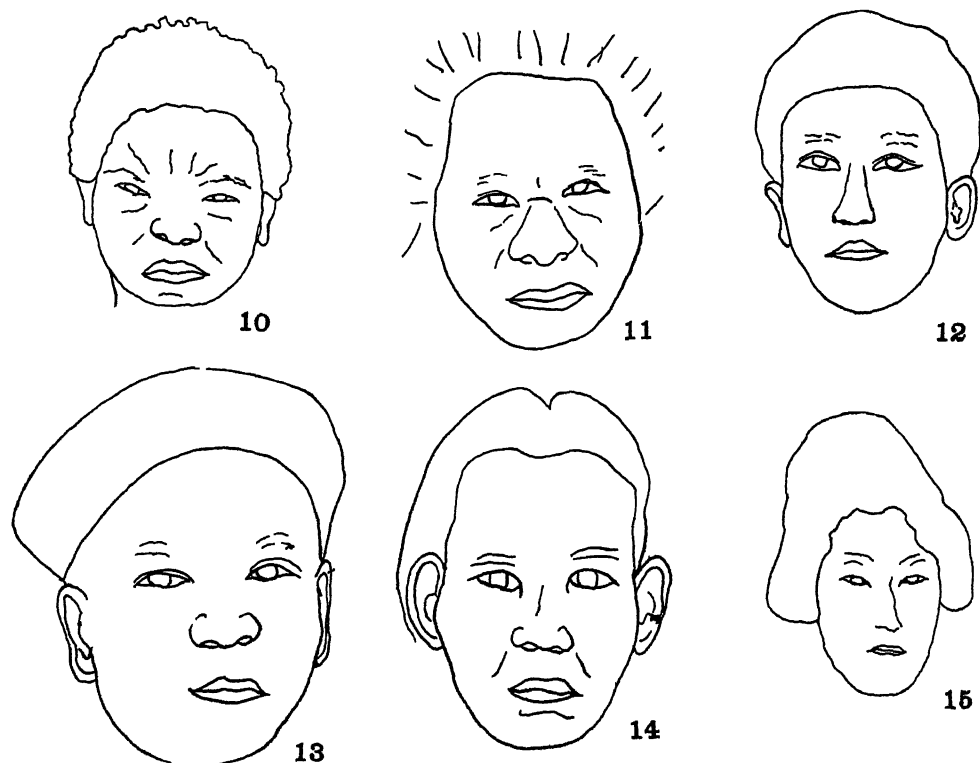


FIG 10 A FILIPINO NEGrito OF THE HYPOMORPH TYPE FIG 11 A MELANESIAN OF THE MESOMORPH TYPE FIG 12 A POLYNESIAN OF THE HYPERMORPH TYPE FIG 13 A CHINESE OF THE HYPOMORPH TYPE FIG 14 A CHINESE OF THE MESOMORPH TYPE FIG 15 A JAPANESE OF THE HYPERMORPH TYPE

Whites from near the Mediterranean, called in India, Pie-Dividiens, and other Whites from the north, called Indo-Europeans. It would take too much time and space to unravel the complexities of such a conglomerate even were it possible. A few characteristic outlines of the face will be given, with a later analysis of a Malay group in averages

are the most characteristic types of the groups. The Negritos are more Hypomorph, the Melanians are more Mesomorph and the Polynesians are more Hypermorph, whereas the Chinese are both Hypomorph and Mesomorph, and the Japanese are Hypermorph among the upper classes although both Hypomorph and Mesomorph among the lower classes

The Negro and the Melanesian are like the Hypomorph and Mesomorph Blacks, which they are in fact, and the Polynesian is like the Hypermorph of the Whites. The Chinese and Japanese are Yellow-Browns. The Mesomorph Chinese is like the Hypermorph Black, and the Hypermorph Japanese is like the Extreme Hypermorph White. Further description of the types is unnecessary if the reader will refer to the descriptions already given for the types among the Blacks.

A great difference was found between the official classes and the laboring classes when examining the Japanese in 1907 and 1910. The percentage proportions of the types are given in table 3.

TABLE 3
The proportions of the types in Japan

CLASS	HYPMORPH	MESOMORPH	HYPERMORPH	NUMBER
Official male	31	26.5	70.4	256
Laborer male	28.1	58.3	13.6	3,812
Both female	27.6	45.5	26.9	442

The difference is so great and so striking that the two classes seem almost to be different races, although both are Yellow-Brown. A photograph is presented in figure 16 of a lady of the upper class who is a true Oriental although much like many Europeans of the Mediterranean stock, of Spanish or even of English extraction. The inference is that insular life during a considerable period of time has produced in the Orient similar types to those of the Occident under similar conditions. As Fleuret (32) has found that the south Britons have become slenderer, so we may presume that the Japanese have done the same, especially in the higher classes.



FIG. 16. A JAPANESE WOMAN OF THE RULING FAMILY, OF THE EXTREME HYPERMORPH TYPE.

From World Wide Photos

We may now present the actual measurements of typical representatives of the Hypomorph, Mesomorph, and Hypermorph Yellow-Browns (table 4).

The differences between the types are obvious from this table of measurements, and verify the descriptive differences

those of the Black types. These are racial differences that are not obscured by the type differences; neither does one set of characters vitiate the other. Both are obvious.

The Blacks have the shortest ears and the broadest noses in the world, and the

TABLE 4
Actual measurements of typical Hypomorph, Mesomorph and Hypermorph persons of the Yellow-Brown Race

	HYPMORPH		MESOMORPH		HYPERMORPH	
	Male	Female	Male	Female	Male	Female
Character:						
Stature.....	149.8	142.1	168.4	152.2	170.7	155.8
Sitting height.....	83.0	75.5	88.1	80.5	88.8	79.0
Leg length.....	66.8	66.6	80.3	71.7	82.5	76.8
Arm length.....	67.3	65.7	79.0	67.8	80.5	70.2
Acromion height.....	120.3	115.2	138.0	122.8	138.7	128.6
Head length.....	17.2	16.3	18.3	17.2	18.2	18.0
Head breadth.....	15.3	14.2	15.6	14.6	14.3	14.1
Head height.....	13.0			12.3	12.4	12.3
Nose length.....	4.6	3.4	4.7	4.6	4.4	4.9
Nose breadth.....	4.1	3.9	4.2	4.0	3.6	3.8
Ear length.....	6.3	5.9	6.7	6.6	6.3	6.3
Ear breadth.....	3.6	3.6	3.8	3.6	3.6	3.2
Index:						
Sitting height						
Stature.....	55.4	53.1	52.2	52.8	51.6	50.7
Sitting height						
Leg length.....	124.0	113.2	109.5	112.3	107.0	102.4
Sitting height						
Arm length.....	123.6	115.0	111.4	118.5	109.5	112.5
Head breadth						
Head length.....	89.0	87.1	85.3	85.0	78.5	78.0
Nose breadth						
Nose length.....	89.1	114.7	89.0	87.0	81.8	77.5
Ear breadth						
Ear length.....	57.2	61.0	56.8	54.6	60.2	50.7

already given. The stature, head breadth and leg length are especially characteristic as are also all of the indices. Attention is directed to certain differences between the types of the Black Race and the Yellow-Brown. The head breadth, nose length and ear length of the Yellow-Brown types are uniformly greater than

Yellow-Browns have the longest ears and the broadest heads in the world. The Yellow-Browns have a high cephalic index and the Blacks a low one. On the other hand the Hypomorph has great head breadth, the Mesomorph less and the Hypermorph least; the Hypomorph has a high cephalic index, the Meso-

morph less and the Hypermorph least; and the Hypomorph has a high nasal index, the Mesomorph less and the Hypermorph least. The ear index is not so good a differentiator of type as the other characters, or as the form of the ear from the descriptive point of view. The descriptive characters of the ear (10) have been used by me more than any other single character, although the nose is equally characteristic, but I have described the ear and nose types in other publications (7) (8) (11) (12) (13) (17),

number of Chinese and Spanish Mestizos among them. Some of those between the ages of 14 and 25 are from Taytay, where all the remainder between the ages of 25 and 80 reside. These are the purest Malays, although they may have a trace of East Indian and Chinese among them. In spite of this conglomerate and in spite of the small numbers at certain ages the tables show fairly uniform differences between the types. The entire group is a fair representation of the Yellow-Brown Race, although there are no American

TABLE 5
Number of Filipinos in each sex, type and age group

TYPE	AGE												
	- 6	- 8	- 10	- 12	- 14	- 16	- 18	- 20	- 25	- 30	- 40	- 50	- 60+
Male													
Hypomorph.....	4	1	2	6	9	14	7	6	5	4	3	2	1
Mesomorph.....	4	8	11	10	19	73	189	117	53	27	22	19	17
Hypermorph	6	2	6	9	10	23	39	26	13	9	16	4	6
Female													
Hypomorph.....		2	1		2	6	9	7	3	2	3	2	
Mesomorph.....			2	7	8	21	20	13	8	7	3	11	5
Hypermorph		1		5	8	7	18	2	4	2	8	6	3

therefore it is not necessary to repeat the descriptions here.

Tables 6 and 7 illustrate by averages the actual measurements of 1,008 Filipinos between the ages of 5 and 80 years. Table 5 shows the number at each age and in each sex.

Three groups of Filipinos are included in table 5. Those under 12 years are from the schools in Manila, residents of that city and largely of the littoral or coast Malays, Neo-Malays. Those between 14 and 25 are students of the Normal and Trade schools in Manila, and from all parts of the Philippines. They are also Neo-Malays, but have a large

Indians among them. The stock from which the American Indians came is well represented, as also are related stocks.

In tables 6 and 7 the male and female statures are shown for the three types. The Hypomorph is of lower stature at all ages than either the Mesomorph or the Hypermorph, and the latter two have nearly the same stature although the stature of the Mesomorph is usually less than that of the Hypermorph. The high stature at the age of 20 years is due to the large number of Mestizo students. The stature after that age is smaller because only the Malays of Taytay are included. The

averages of the females are more irregular than those of the males because of fewer females at each age.

the types as those of the stature, although not so clearly. The female is particularly irregular and in the early years the

TABLE 6
Average measurements of Filipinos and Whites (males) between the ages of 5 and 80 years
Dimensions are in centimeters

	AGE													
	- 6	- 8	- 10	- 12	- 14	- 16	- 18	- 20	- 25	- 30	- 40	- 50	- 60	- 70
Stature														
Filipino hypomorph.....	—	104	115	131	140	143	152	157	152	151	152	152	152	152
Filipino mesomorph.....	110	115	123	134	149	159	164	168	167	159	159	159	162	—
Filipino hypermorph.....	106	121	126	137	138	158	168	164	166	161	163	162	166	160
White mesomorph.....	115	119	131	140	150	—	166	171	173	173	171	172	170	—
White hypermorph.....	120	124	134	143	155	—	175	176	177	178	175	176	176	174
Sitting height														
Filipino hypomorph.....	58	59	61	68	70	78	81	83	82	82	81	82	81	78
Filipino mesomorph.....	59	62	64	68	76	82	84	84	85	84	84	85	84	—
Filipino hypermorph.....	56	61	65	70	77	82	85	86	86	84	87	86	86	81
White mesomorph.....	62	63	68	72	76	—	89	91	93	93	93	93	93	91
White hypermorph.....	62	64	68	73	78	91	90	93	94	94	93	94	94	92
Leg length														
Filipino hypomorph.....	49	45	51	63	71	73	71	73	71	70	70	71	—	—
Filipino mesomorph.....	—	55	58	64	73	77	78	79	78	75	76	75	76	—
Filipino hypermorph.....	—	54	61	66	76	79	81	78	78	75	77	80	78	77
White mesomorph.....	54	56	64	69	73	—	79	83	84	84	81	81	79	—
White hypermorph.....	57	61	67	71	77	—	—	86	85	85	85	85	84	81
Leg index														
Filipino hypomorph.....	119	116	114	108	102	105	114	113	113	121	113	116	—	—
Filipino mesomorph.....	117	113	109	108	105	106	107	107	109	113	112	115	114	111
Filipino hypermorph.....	115	110	105	107	100	105	107	109	109	113	114	112	110	—
White mesomorph.....	118	115	108	106	106	—	—	108	110	112	114	115	116	—
White hypermorph.....	106	106	105	102	103	—	—	104	106	108	107	110	111	—
Hand length														
Filipino hypomorph.....	—	—	—	—	—	148	178	172	168	163	164	163	157	—
Filipino mesomorph.....	—	—	—	—	—	168	178	178	178	177	179	180	181	—
Filipino hypermorph.....	—	—	—	—	—	171	166	188	184	178	181	181	181	178

The averages of the male and female sitting height as shown in tables 6 and 7 illustrate the same differences between

averages almost coincide. The differences are clearer in the males. Here, as in the stature, the Hypomorph has a lower

sitting height at practically all ages types, although in the female, as usual, than the Mesomorph and Hypermorph, the difference is not so clear as in the and the latter two are close together. male. The sexual factor in the female

TABLE 7
Average measurements of Filipinos and Whites (females) between the ages of 5 and 70
Dimensions in centimeters

	AGE														
	- 6	- 8	- 10	- 12	- 14	- 16	- 18	- 20	- 25	- 30	- 40	- 50	- 60	- 70	
Stature															
Filipino hypomorph.....	114	121	125	137	145	145	151	150	150	145	145	140	—		
Filipino mesomorph.....	—	—	—	140	148	152	154	154	154	147	149	144	144	144	
Filipino hypermorph.....	—	116	125	140	149	154	154	156	151	151	150	150	146		
White mesomorph.....	117	121	130	140	150	156	—	161	163	160	160	160	160	160	
White hypermorph.....	118	123	132	146	156	160	163	163	163	163	164	165	163	161	
Sitting height															
Filipino hypomorph.....	—	61	66	73	78	78	81	81	81	78	78	77			
Filipino mesomorph.....	—	—	—	73	75	78	79	80	82	79	79	78	76	76	
Filipino hypermorph.....	—	59	65	72	76	81	81	84	80	81	80	79	79	—	
White mesomorph.....	61	62	67	75	79	81	—	—	87	86	88	86	87	85	
White hypermorph.....	63	66	69	75	81	84	—	—	86	86	86	87	87	84	
Leg length															
Filipino hypomorph.....	—	55	57	65	70	67	70	69	70	69	68	67	—	—	
Filipino mesomorph.....	—	—	—	67	73	73	74	73	73	68	70	70	70	68	
Filipino hypermorph.....	—	60	63	67	71	72	73	72	72	72	72	72	65	—	
White mesomorph.....	53	57	62	68	73	73	—	—	76	76	73	73	72	—	
White hypermorph.....	54	59	64	71	76	78	—	—	77	77	79	79	79	78	
Leg index															
Filipino hypomorph.....	—	113	112	111	110	113	112	114	113	114	111	112	112		
Filipino mesomorph.....	117	114	111	108	103	107	107	110	112	114	112	112	111		
Filipino hypermorph.....	—	—	—	107	105	111	109	116	114	116					
White mesomorph.....	117	109	108	105	107	106	—	—	117	118	122	117	118	116	
White hypermorph.....	118	112	104	105	106	105	—	—	111	107	111	111	111	111	
Hand length															
Filipino hypomorph.....							172	161	157	145	166	160			
Filipino mesomorph.....									155	162	162	162	161	158	
Filipino hypermorph.....									168	178	158	168	158	168	

The averages of the male and female leg length as shown in tables 6 and 7 illustrate more clearly than those of sitting height the difference between the may have something to do with the irregularity of the data, although the small number of persons may also be responsible. The greatest difference so far noted is in

the short legs of the Hypomorph in relation to the leg length in the other two types. This is one of the chief differences noted between the types.

The averages of the male and female leg index, or the sitting height divided by the leg length, as given in tables 6 and 7 show differences between the Hypomorph and Hypermorph, with the Mesomorph in between, during the earlier years especially; but there is some irregularity in the adult and preadult stages. These averages fall as the legs grow rapidly and rise as the sitting height grows rapidly. The Hypomorph average is above the others in the male and also to some extent in the female.

The averages of the male and female hand length as shown in tables 6 and 7 illustrate the differences between the three types in this respect. The Hypomorph has a short hand, the Mesomorph is intermediate and the hand of the Hypermorph is long. The hand of the Hypomorph is also broad, that of the Mesomorph is intermediate, and the hand of the Hypermorph is narrow. The Chinese have long narrow hands, therefore the index of the hand, the width divided by the length, would be Hypermorph. It is about 40 in the Chinese; whereas it is about 42.5 in the American White Hypermorph and about 45 in the American White Mesomorph. The hand breadth of the Filipinos was not measured, but from observation the hand index of the Hypomorph Filipino is between 45 and 50.

Tables of averages of the same kind as those given have been made for such characters as the head height, head breadth, head length, cephalic index, mean head height index, head height-head length and head height-head breadth indices, nose length, nose breadth, nasal index, ear length, ear breadth,

ear index, upper arm length, lower arm length, brachial index, hand length, hand breadth, upper leg, lower leg, crural index, intermembral index, leg-sitting height index, arm-sitting height index, and others. In all of these the three types may be separated more or less. When it is considered that the types were determined chiefly by the careful inspection of the ear and nose form, it will be understood that the types are anthropometric entities as well as morphologic forms. The measurements and curves corroborate the evidence of the eye. It is of great interest and importance that the type holds together so well. In rare individuals there is a mosaic. Sometimes the head will be Hypomorph and the arms and legs Hypermorph, again the head will be Hypermorph and the arms and legs Hypomorph. Then again the ears will be of one type and the nose and body of another, and so on. There are also blends and fusions of many degrees, making an almost interminable variety of forms. The Hypomorph and Hypermorph are the extremes, and they are selected with more care than the Mesomorph, because among the Mesomorphs are included mixed and mosaic forms.

III. TYPES OF THE WHITE RACE

Aristotle (50) taught that "The first principles are fire, air, water and earth, for from them are formed all living things and the productions of the earth: they are therefore called elements," but Aristotle also said "In general it is silly to rely on a single sign: you will have more reason for confidence in your conclusions when you find several signs all pointing the same way." Hippocrates (1) used the temperaments throughout his practice, and considered the different characters of the races of man as the result of

environment. The strongest natural causes of variability in man were the seasons, then the country, and the waters, according to Hippocrates. Both he and Galen taught that the different kinds of moisture in man's body, phlegm, blood, choler and melancholy, as they predominate, determine the temper of the mind. "An exact balance of the four humors makes a justly constituted man, and allows for the undisturbed processes of digestion and assimilation." The School of Salerno (40) which flourished during the crusades was a Mecca for great physicians as well as celebrated patients and taught the four temperaments of Hippocrates. Albrecht Dürer depicts the four temperaments in the form of four apostles, and they have been variously represented by other great artists.

The temperaments as depicted by Albrecht Dürer, and as taught at the School of Salerno, based upon the four elements of Aristotle, air, earth, fire, and water and upon the four humors of Hippocrates blood, black bile, yellow bile and phlegm, and known as the sanguine, melancholic, choleric, and phlegmatic, may not be generally accepted; and the rheumatic, catarrhal, phthisical and plethoric diatheses may have a greater significance, but doubtless all of these four categories in relation to man refer to four races that may have been recognized early in the history of Europe. The fiery Spaniard or other Mediterranean people may represent the choleric temperament, the Nordic the sanguine, the Celts were phlegmatic, "fair and white," while the Alpines were both "swart and colly," dark and melancholy. The races may have been more distinct in the time of Hippocrates than at present, because at present mosaics and blends are numerous and even the four races are not distinct. One may select the four races from a large

group, but they will show great variability.

An investigation of students was made at the University of Michigan in 1906, and this was followed by a similar study at Tulane University in 1913, and since then at the University of Virginia. Nearly 2,000 students were measured and examined. An attempt was made to select from these the ones that conformed to the four races, with the results as given in table 8.

The approximate proportions of different nationalities in the ancestry from casual memory of the students was: English 37 per cent, German 11 per cent, Scotch 10 per cent, Dutch 8 per cent, French 5 per cent, and the remainder scattering over many nations. The class standing in the Freshman year was: Celt about 85, and Alpine, Nordic and Mediterranean about 75.

The important findings from this study are that only about 60 per cent of all the students could be considered as belonging to the four races, and there is great variability so that each group is hardly an entity, but a conglomerate of variables. The four races represent only two morphologic forms because the Nordic and Mediterranean are very much alike except in pigmentation, as are the Celt and Alpine. The remaining 40 per cent of the students present so many mixtures, blends and mosaics that it was almost impossible to classify them with the four races, but they could be fairly well grouped into the two morphologic forms.

Measurements of school children and Old Americans (49) were made later,—the Old Americans during the past few years,—and averages from these measurements may be seen in tables 6 and 7. Each person was grouped as a Mesomorph or as a Hypermorph, although a more striking difference might have been revealed

if they had been grouped as the Filipinos were, into two, small, extreme groups and a large intermediate one. Two sets of people were utilized for the tables,—about 1,500 school children of Ann Arbor, Michigan, and about 2,000 Old Americans (49) recently measured in Virginia. Only the British-American children of Ann Arbor, and only the most recently examined Old Americans of Virginia were used. The two groups

morph Filipino comes close to that of the Mesomorph White.

The sitting height (tables 6 and 7) is in general greater in the Hypermorph than in the Mesomorph but the difference is not so great as in the stature. The difference between the Filipino and American White is slight except in the adult.

The leg length (tables 6 and 7) is greater in the Hypermorph than in the

TABLE 8
Characters of the four European races

CHARACTERS	NORDIC		MEDITERRANEAN		ALPINE		CELT	
	Average	Variability	Average	Variability	Average	Variability	Average	Variability
Male								
Body:								
Weight.....	66.3K	±7.3	63.1	±7.2	63.1	±7.2	65.9	±6.7
Per cent pigment.....	35.4	±12.7	87.1	±12.4	84.5	±9.9	37.1	±12.5
Stature.....	174.4	±5.4	170.8	±5.8	169.4	±5.0	174.6	±3.1
Chest circumference.....	88.0	±5.4	86.0	±5.2	87.4	±5.4	87.8	±4.9
Head:								
Length.....	19.9	±0.6	19.8	±0.7	19.2	±0.7	19.2	±0.7
Breadth.....	15.5	±0.4	15.5	±0.4	16.0	±0.5	16.1	±0.5
Cephalic index.....	76.5	±2.5	76.8	±2.2	81.4	±2.3	83.6	±2.1
Female								
Body:								
Weight.....	53.4		52.4		47.8		53.0	
Per cent pigment.....	32.8		87.0		91.0		25.0	
Stature.....	163.0		158.8		157.0		161.0	
Chest circumference.....	78.5		75.0		73.7		79.0	

are fairly comparable although only in the Old Americans was the ancestry for two generations obtained.

The stature as given in tables 6 and 7 is greater at all ages in the Hypermorph than in the Mesomorph, and the difference is greater in the adult than in the children, and greater in the male than in the female. The stature of the American Whites is greater than that of the Filipinos, although the stature of the Hyper-

Mesomorph, and the difference is considerable in both sexes at all ages.

The leg length index (tables 6 and 7) is extremely different in the two types especially in the adult. This index shows that the hypermorph has long legs and the Mesomorph short ones with the sitting height reversed, the Hypermorph short and the Mesomorph long.

More than 40 charts have been prepared of measurements and indices of the vari-

ous parts of the body, and they all show differences between the Hypermorph and Mesomorph, some of which have already been given in this paper. Some of the

TABLE 9
Actual measurements of typical Hypermorph and Mesomorph persons of the White Race

	HYPERMORPH		MESOMORPH	
	Male	Female	Male	Female
Character:				
Stature.....	172.1	166.6	180.0	163.3
Sitting height	89.8	87.6	95.7	88.6
Leg length.....	82.3	79.0	84.3	74.7
Arm length.....	80.1	73.1	78.3	69.7
Acromion height.....	143.5	141.0	150.8	136.1
Head length.....	19.5	19.5	20.0	19.7
Head breadth.....	15.1	13.6	14.8	14.3
Head height.....	13.4	13.5	13.3	14.1
Hand length	20.5	17.7	19.5	17.1
Hand breadth.....	8.5	7.8	9.1	7.9
Nose length	5.9	5.7	5.3	4.9
Nose breadth.....	3.3	3.0	4.1	3.7
Ear length	6.1	6.0	7.0	6.3
Ear breadth.....	3.6	3.6	4.4	3.6
Indices:				
<u>Sitting height</u>				
Stature	52.0	52.5	53.1	54.3
<u>Sitting height</u>				
Leg length	109.0	110.5	114.0	118.0
<u>Sitting height</u>				
Arm length	112.0	119.5	122.0	127.0
<u>Head breadth</u>				
Head length	77.5	69.8	74.0	72.6
<u>Head breadth</u>				
Hand length	42.3	44.0	46.7	46.2
<u>Nose breadth</u>				
Nose length	55.9	52.5	77.3	75.5
<u>Ear breadth</u>				
Ear length	59.0	60.0	63.0	60.3

differences are presented in table 9 as they appear in typical individuals.

The characters show the differences between the types except for the head and ear. The cephalic and ear indices

are the least reliable of all characters in the differentiation of types. The nasal index is probably the best indicator of type. It is to be noted that the Hypermorph male is smaller than the Mesomorph. This is because an extreme Hypermorph was selected. The extreme Hypermorph is more slender than the normal Hypermorph and is also smaller, and the stature is much less in the most extreme cases.

Illustrations of the Hypermorph type are presented in figures 17, 18, 21, 22, 27 and 28, and of the Mesomorph type in figures 19, 20, 23, 24, 25, and 26. The differences that have already been described are obvious.

There is a pathological form that has been called Mongolian Idiot or Mongol, a better term for which would be Mongoloid Dwarf, which occurs in all of the three races, White, Black and Yellow-Brown, and has some of the characteristics of the Hypomorph. This type is illustrated in figures 29 and 30. Crookshank (26) has tried to prove for them inheritance from Mongolians who came into Europe at an earlier period. It is possible that it may be a form that is being eliminated by a lethal factor. Mongoloid Dwarfs usually die young, are extremely susceptible to acute infections, and all the tissues seem to be defective and deficient. A table (table 10) of some of the characters of the Mongoloid Dwarf is given to show that they are Hypomorph.

IV. DISCUSSION

Human types may be discussed under three heads, racial types, morphologic or anatomic types and physiologic types.

The definition of a Race has been conceived in divers ways, at different times, by various men. That of de Quatrefages (29b) is one of the oldest and best.



FIG. 17. AN AMERICAN WOMAN OF BRITISH-FRENCH EXTRACTION OF THE HYPERMORPH TYPE. FIG. 18. SIDE VIEW OF THE SAME. FIG. 19. AN AMERICAN WOMAN OF BRITISH-DUTCH EXTRACTION OF THE MESOMORPH TYPE. FIG. 20. SIDE VIEW OF THE SAME



FIG. 21. AN AMERICAN MAN OF THE HYPERMORPH TYPE. FIG. 22. FRONT VIEW OF THE SAME. FIG. 23. AN AMERICAN WOMAN OF THE MESOMORPH TYPE. FIG. 24. SIDE VIEW OF THE SAME



FIG. 25. FRONT VIEW OF AN AMERICAN MAN OF BRITISH ANCESTRY OF THE MESOMORPH TYPE. FIG. 26. SIDE VIEW OF THE SAME. FIG. 27. FRONT VIEW OF A SPANIARD OF THE EXTREME HYPERMORPH TYPE. FIG. 28. SIDE VIEW OF THE SAME. FIG. 29. FRONT VIEW OF A MONGOLOID DWARF OF THE WHITE RACE. FIG. 30. SIDE VIEW OF THE SAME.

TABLE 10

Measurements of a typical Mongoloid Dwarf woman, aged 25, and man, aged 28

	FEMALE	MALE
Character.		
Stature	139 9	146 3
Sitting height .. .	81 1	83 6
Leg length .. .	58 8	62 7
Arm length . . .	58 0	59 3
Acromion height .. .	116 8	120 3
Head length	16 7	16 8
Head breadth .. .	14 3	15 2
Head height	12 7	13 3
Nose length. . .	4 7	4 7
Nose breadth	3 5	3 4
Ear length . . .	4 7	6 0
Ear breadth	3 3	3 4
Indices:		
Sitting height		
Stature	58 0	57.1
Sitting height		
Leg length	137.8	133 5
Sitting height		
Arm length	139 2	141 0
Head breadth		
Head length	85 6	97 8
Nose breadth		
Nose length	74.6	72 3
Ear breadth		
Ear length	70 4	58 3

A *Species* is a group of individuals, more or less resembling each other, that are descended, or that ought to be regarded as having descended, from a single primitive pair by a natural and uninterrupted succession of families.

A *Variety* is an individual or group of individuals pertaining to the same sexual generation, that is distinguished from other representatives of the same species by several exceptional characters.

A *Race* is a great group of people who have had the same origin; who have spread over a large area of the earth; and who resemble one another in a great many stable characters.

A *Races* is therefore only part of a broken up *Species*.

Hooton (44) has within the year defined a Race as "a great division of mankind, the members of which, though individually varying, are characterized

as a group by a certain combination of morphological and metrical features, principally non-adaptive, which have been derived from their common descent."

He then gives a list of characters that are principally non-adaptive. Some of these are subject to sexual selection and should be omitted. Other characters that are modifiable and may be remodified might be added. Then we would have as the best differential characters the following: Hair form, sutural patterns, postglenoid tubercle, pharyngeal fossa or tubercle, form of incisor teeth, form of the vertebral border of the scapula, supracondyloid process or foramen, the crural and brachial indices, bowing of the radius and ulna, nasal index, hard palate, height of head, volume of brain, proportions of thorax, relative length and angle of the heel bone, and size and development of the calf muscles. To these might be added the form of the external ear, and of the nose, and the hand index, although there may be some objection to them, as being either modifiable or sex selected. I agree with Hooton that this list offers a good working basis, and that his definition of a Race is a good one.

De Quatrefages (19b) divided man into three races, White, Black and Yellow, with the Oceanic and American as mixed races; not that color is the most important character that differentiates them, but that it is easily seen and understood. Haddon (39) uses terms of hair form to distinguish the three races; this is a better differential character than the skin color. Hrdlička groups the Oceanic and American peoples with the Yellow race as the Yellow-Browns, and this is justified because of their origin, although a large Negro element is to be found in Oceania, and also in southern Asia.

According to Hooton (39) a race is a

"great division of mankind," therefore he may exclude all but the three great races of man. Other peoples such as the Australians, Ainos, and Eskimos are remnants or fragments of man who have been isolated under peculiar conditions and have inbred more or less until they have in small numbers become quite homogeneous. Groups of a similar kind exist in a more or less isolated condition and may be segregated as Sergi (61) segregated the Mediterranean Race, or Peake (57) the Prospector type, or Ranke the Big-cerebellum-box-headed-Bavarian, or as the type of Beddoe, of Deniker (29), of Ripley (59), of Dixon (30), and of a great many others have been segregated.

Sergi (61) distinguishes many types of skulls as Mediterranean by an elaborate classification and with laborious perseverance, and some verity. He was the first to establish the Mediterranean Race (?) as a distinct entity, yet there are many characters besides those of the skull that have been utilized to differentiate this race.

Peake (57) describes the Prospector type in such a way as to resemble a specialized Alpine stock similar to the Adriatic of Deniker,—tall, heavy, broad, dark, a leader in business and probably wealthy.

The Big-cerebellum-box-headed-Bavarian of Ranke as described by Beddoe speaks for itself.

Deniker (29) divided Europeans into six types or as he called them, races, and four sub-races: 1) Nordic and Sub-Nordic; 2) Eastern, the same as the Celt above, and Sub-Eastern or Vistulian; 3) Ibero-Insular or Mediterranean, or *Homo meridionalis*; 4) Western, Cevenole or Alpine, also called Celtic, Celto-Slav, Rhetian, Ligurian, or Celto-Ligurian; 5) Littoral, Atlanto-Mediterranean, or Cro-Magnon, and Sub-Littoral or Northwestern; 6) and Adriatic or Dinaric, and

Sub-Adriatic similar to the Sub-Nordic although semi-Alpine. The Littoral is an enlarged Mediterranean or a modified Cro-Magnon, and the Sub-Littoral is a mixture of Nordic and Mediterranean. The Adriatic is an enlarged Alpine type, and the Sub-Adriatic is a mixture of the Alpine and Nordic. This is one of the best classifications of the types of Europe, but it takes in several local varieties. More types could be added, or the types could be grouped into fewer varieties.

The work of Ripley (59) is exhaustive and very good because it confined itself to the few fundamental types that may be distinguished, and located them in a general way. The Alpine, Nordic and Mediterranean represent at least recognizable types, but Ripley shows too much or too little. Too much stress is laid on cephalic index, stature and pigmentation. Too little stress is laid on non-adaptive characters. All the people of Europe are not Alpine, Nordic or Mediterranean. Many varieties are to be found. Nor will all the varieties together include all the people.

Other methods than those used by Ripley and Deniker must be utilized to get at the true conditions. On the strength of this, when I first examined the students at the University of Michigan, and later the students in Manila, at the University of the Philippines, I grouped them as if they were polyhybrids resulting from a cross of two different stocks. I obtained eight forms that showed almost the same percentage proportions as those obtained by Price and Drinkard upon the crossing of the Yellow Pear with the Honor Bright Tomato, and almost the theoretical requirements for a Mendelian trihybrid.

This method was discarded because it was inadequate to explain all types, and because too few characters could be used.

Dixon (30) has recently applied the same method to a study of the distribution of human types from a few factors of skull form. There is a great deal of truth in his results, some of his types are entities, but not enough characters were used; his material was inadequate; and he did not select non-adaptive characters. After we have learned more about the intricate details of Mendelian inheritance we may hope by the use of proper methods, proper characters and studies through three or more generations of living men to attain satisfactory results.

Günther (38) has recently classified the races of Germany as Northern or Nordic, Western or Mediterranean, Eastern or Alpine, and Dinaric. The physiognomy of the Dinaric is striking and more or less uniform in his numerous illustrations, but the type seems to be similar to the Littoral of Deniker, and Deniker calls his Littoral type Dinaric. The head is short and high like the Armenoid head and some artificial deformation is suggested by its appearance.

The evolution of man from the Neanderthal form that existed in Europe about 30,000 years ago is being more surely traced as new discoveries are made. Scattered forms throughout Europe, such as the Spy skeletons (47), the Chancelade skeleton (56), Aurignacian forms (47), the Krapina finds (36), and more recently the discoveries in Bohemia (52) and Moravia (63) which have not yet been fully worked over and completely described, give assurance that these forms continued to our day in modified condition, changing through the Brno, Brück, Combe-Capelle, Cro-Magnon and later types into the modern types of Europe (70).

Hrdlička has repeatedly called attention to this in his public and private lectures. Man has evolved in masses

and in isolated groups, with modifications of one kind or another, into multiple forms in Europe. In some places the primitive forms have been retained more or less modified as in some of the islands of Denmark (64) where Neanderthaloid forms have been measured in anthropometric surveys. In other places the forms have become extremely different from the original, as in the transformations from the Combe-Capelle type to the small, slender stock, as traced and described by Fleure (32) in Wales and Ireland. Some of the Combe-Capelle stock has remained less modified than others, producing what has been called the Old Black Breed of Scotland, Ireland and Wales.

There has been a gradual change in the different continental and coast areas that makes the interior peoples of Europe different from the coast peoples. The heavy, stocky kind of the interior is different from the small slender kind of the coast. Thus we have the Mesomorph and the Hypermorph respectively.

Montelius (55) traces the present stock of Nordics in Sweden to the prehistoric form found there 10,000 years or more before our time, and probably derived from a form similar to the Cro-Magnon in France. There is evidence of the persistence of the Cro-Magnon (29a) in France today in Dordogne where disharmonic types may be seen (59). No doubt this type spread in western Europe becoming modified with changing conditions. The same stock spread into Asia, and the Steppe folk of Peake belong to this stock.

Hrdlička (48) concludes from a study of the peopling of Asia that the earliest people were Negritos from Africa; the next stock was the "Australoid" from a form in Europe like the Aurignacian and late paleolithic; the rest of the popula-

tion came from the west, northwest, and north, spreading in waves with subsequent mixture. This population gradually spread over the whole of Asia and out into the seas, across Japan, and over variable practicable routes to America, some of it from the Pacific Islands, some through Alaska. The Negro and Negrito are from the old Mediterranean and European stock at an earlier period than the movement into Asia, probably early Neanderthal, and as they moved through Africa they developed into the big Negro and the little Negrito. The earliest known cradle of humanity was in Western Europe. My own conclusions have been practically the same from a study of the living, although carried out independently and in a different way.

It would appear that a big and a little stock are apt to develop from the same original, as the Cro-Magnon and the Combe-Capelle, the Nordic and the Mediterranean. Then other forms come from these. The round heads seem to come from the long heads. The long headed Negroes produced the round headed Negritos, the long headed Europeans produced the broad headed. The Nordic produced the Celt, the Littoral produced the Alpine, and the Mediterranean has produced a small, broad headed, short nosed, short faced stock that is frequently confused with the Alpine. The broad heads of Mugem, Furfooz, and other places may be Mediterranean rather than Alpine.

Harold Peake (57) has recently traced the Bronze Sword and Iron Sword people through Europe from about 4000 B.C. almost to our era. About 4000 B.C. Alpine peoples occupied the mountains of central Europe, coming originally from Asia Minor, and Nordic-Steppe folk mounted on horses were driving cattle from pasture to pasture over steppe,

and through forest. About 3000 B.C. a drought caused some of the steppe folk to emigrate and they reached the Baltic, Belgium, Switzerland and Hungary. This was followed by other emigrations. The first emigrants had leaf-shaped bronze swords, and as they conquered they mixed with the Alpines producing a Celtic stock that was partly blond. They conquered nearly all of Europe except the Iberian peninsula. Later the Iron Sword people of the same Nordic-Steppe stock conquered almost all of Europe, but not Scandinavia or Britain. The Nordic-Steppe people were like the Kurgan builders of Russia, the people of the Row Graves in Germany, not unlike the Scandinavian Nordic type and the Vikings, similar to a modified form of the Cro-Magnon, and may have had some part in forming the Littoral, Adriatic, and Dinaric types. A stock similar to this has been found among the Himalayas, as in the Sikhs, and among the American Indians. Stocks like the Turks as they were originally, and some of the eastern African peoples were much like these steppe folk. They may be called the Conquering Race because they moved from place to place conquering as they went. Measurements of two persons derived from that stock as found at present in America are given in table II.

The Conquering Race is of the Hypermorph type and may be blond or brunette. They are not the extreme Hypermorph which is small and slender and also blonde or brunette. More of the extreme Hypermorphs in America are brunette than blond and more of the Hypermorphs are blond than brunette.

The characters of the Conquering Race are like those of the Caspian Race of Dixon (30) and there is evidence of a distribution of the living similar to that found by him in studying the skeletal

remains. The stock was tall, large boned, long limbed, long headed, large faced, and big nosed. They became more slender, and their physiognomy changed in Europe. They spread over Europe in the late paleolithic period, and from the

TABLE II

Actual measurements of a man and woman of the Conquering Race now living in America

	MALE	FEMALE
Character:		
Stature.....	183.0	171.3
Sitting height.....	95.0	89.6
Leg length.....	88.0	81.7
Arm length.....	87.0	78.9
Acromion height.....	154.0	145.7
Head length.....	20.0	19.9
Head breadth.....	15.1	15.0
Head height.....	14.4	14.8
Hand length.....	19.6	19.0
Hand breadth.....	9.3	8.3
Nose length.....	6.2	5.5
Nose breadth.....	3.1	3.7
Ear length.....	5.8	5.8
Indices:		
<u>Sitting height</u>		
Stature	52.0	52.3
<u>Sitting height</u>		
Leg length	110.0	110.0
<u>Sitting height</u>		
Arm length	119.2	113.0
<u>Head breadth</u>		
Head length	75.5	75.3
<u>Hand breadth</u>		
Hand length	47.8	43.6
<u>Nose breadth</u>		
Nose length	50.0	67.3
<u>Ear breadth</u>		
Ear length	62.0	60.0

steppes of Asia they came back into Europe. They went north through Siberia to America, and south to the Himalayas and the Pacific, some going into eastern Africa. Their primary characters have been retained more or less in America, the Himalayas, eastern Africa,

and remote places, but in Europe they have become altered. Their color is black in Africa, grayish yellow in Asia and America, and blond or brunette in Europe. This type is closely related to the small, slender Mediterranean type and together they form the most distinct part of the Hypermorph type in Europe, as the Alpine forms the most distinct part of the Mesomorph type.

Having discussed at some length the conditions of race we may now present a few of the conditions of type or anatomic form. Stratz (65) divided man into three groups, *Protomorphs* or nature folk, *Archimorphs* or highly differentiated peoples, and *Metamorphs* or mixed stocks. The Protomorphs comprise the Australian, Papuan, Hottentot, American Indian, Eskimo, Philippine Negrito, and the Negrillo. As some of these are mixed the classification is not consistent. The Archimorphs are the white, the black and the yellow. We come back to the same classification as that of the races.

Manouvrier (54) was the first to show that two European types exist. He called these the Brachyskéle and Macroskéle with the Mesatiskéle in between. The Brachyskéle is broad in every horizontal measurement, and short in every vertical measurement, but especially in the extremities; and the Macroskéle is narrow in every horizontal measurement and long in every vertical one.

Godin (34) extended the work of Manouvrier on the adult in his own investigations on children, and showed that the differences increase with age. The chief difference is in the leg length in relation to sitting height, or sitting height index. The Brachyskéle has relatively short legs and the Macroskéle relatively long ones. The Brachyskéle and Macroskéle, as selected, represent only the two extremes of the population.

By such a selection greater differences might be shown than by taking each person as was done in tables 6 and 7 for the Mesomorph and Hypermorph. The latter represent the same types as the other two above.

Goldthwait (35) in the Shattuck Lecture for 1915 discussed the types of the White race, dividing them into Broad-back and Narrow-back. He found that the Broad-back was inclined to certain diseases more than the Narrow-back, and the latter to certain other diseases more than the Broad-back. The Broad-back and the Narrow-back are the same as the Mesomorph and Hypermorph and the Brachyskéle and Macroskéle respectively.

Treves (67) studied 200 species of animals in relation to the evolution of the intestinal canal, and concluded that the evolution of different species depends largely upon food environment. He divided them into carnivore, with short intestine, and herbivore, with long intestine. The same condition applies to man where the long lean kind has a short intestine and the broad stocky kind has a long intestine.

Bryant (21) (22) took up this work and from a study of autopsies and the dietary relations suggested more than 100 differences between the two types, —anatomical, physiological, chemical and pathological. There can be no doubt of the value of such work in relation to diagnosis, treatment and prognosis of disease.

Stockard (66) suggests the names Lateral and Linear for two types that are the same as the Mesomorph and Hypermorph, and suggests that the former is low thyroid and the latter high thyroid. The distribution of the types seems to make the suggestion plausible because the Mesomorph is found in continental

interiors and the Hypermorph along the coast. Lack of iodine in the interior and presence of iodine in sea water and sea food may account for the differences between the types, at least for the most striking differences. One cannot exclude other factors such as food, climate and habits. The short intestine of the Hypermorph may be the result of concentrated food, and the long intestine of the Mesomorph the result of coarse food of great bulk. The infantile condition of the Hypomorph may be the result of the adverse environment of arctic and tropic regions.

Draper (31) has studied man in relation to disease by reversing the usual anthropometric method of approach. He measured the individuals who had certain definite diseases such as tuberculosis, gastric ulcer, gall bladder infection and pernicious anemia. The result was to find a gall bladder type, a gastric ulcer type, and so on. The gall bladder people in general represent the "sthenic, lateral, or breitwuchs" type and the ulcer cases the "asthenic, linear, or hochwuchs" type. "The ulcer people can never raise their ponderal index above a certain low figure." The ponderal condition of overweight in the gall bladder cases undoubtedly represents a constitutional factor. "The noses of gall bladder people are large in both length and breadth," whereas "the asthma and tuberculosis people have long thin noses." "The ulcer and tuberculosis people have very flat chests, while the gall bladder and pernicious anemia people have deep ones." "The lateral thoracic diameter of the gall bladder people is the greatest. The male pernicious anemia people show the next largest. The tuberculosis and ulcer people have the narrowest chests among the females, and the nephritis hypertension group have the smallest

lateral thoracic diameter among the males. There is a sexual difference in other ways that will be noted later. The tuberculosis and ulcer group in general have flat and narrow chests and the pernicious anemia and gall bladder people have wide and deep chests. The gall bladder and pernicious anemia people have short broad hands, but the tuberculosis, nephritis, and ulcer folk have long narrow hands. The pelvis is broadest in the gall bladder and pernicious anemia people, and the asthma and tuberculosis people have narrow pelvises. The above is taken practically verbatim from Draper. It may be seen that the people who have tuberculosis and ulcer have characteristics of the Hypermorph whereas those with pernicious anemia and gall bladder troubles are decidedly of the Mesomorph type. In previous studies (11), (12), (13) of several thousand cases the author showed that tuberculosis and ulcer occur almost entirely in the Hypermorph type, and gall bladder troubles more frequently in the Mesomorph. Not enough cases of pernicious anemia were studied to decide to what type they belong.

Draper brought out some interesting sexual relations in disease and type. "The male and female of the nephritis hypertension people approach one another in their absolute measurements," but "there are only two measurements in the whole series in all the diseases that show practically no sex difference," "The tuberculosis and ulcer people show great differences in point of size in their absolute measurements. But the two sexes are built in practically identical proportions." In some cases the sex characters seem to be suppressed, in others they are paramount.

The physiological aspects of human types are bound up in diathesis, consti-

tution, habitus, temperament and the like. The corset makers of a previous generation had considerable knowledge of human types. There was a small slender and a tall slender form, a small stocky and a tall stocky form, a form like a pyramid and another like an inverted pyramid, a form like an inverted pyramid with the base of a normal pyramid opposed to it, or big in the middle and small at each end, and finally the opposite of the last, a form large at both ends and small in the middle. The first two of these types are Hypermorph and the next two Mesomorph. The other four types are not so common and represent mosaics.

Among the first to call attention to four physiological types are Chaillou (24) and his coworker Mac-Auliffe (25), although they give the credit to Sigaud (62) who originated the terms respiratory, digestive, muscular, and cerebral types. They also call attention to the work of Tricolet (68) on four similar types. These types have become well recognized and are utilized in medical clinics, therefore a few words about each may not be out of place.

Muscular type. The face is rectangular, vertical in front, no prognathism, and the distance from the top of the forehead to the glabella, from the glabella to the nasal spine, and from the latter to the chin are equal. These three parts of the face differ in the other types. The upper part is large in the cerebral type, the middle part in the respiratory, and the lower part in the digestive. The nose in the muscular type is straight or sinuous, high and somewhat rectangular. The neck is broad, well filled with muscle, but not necessarily short. The shoulders are horizontal as are the clavicles and acromion processes. The iliac crests are not very wide, but the costal angle is

about 80°. The profile of the trunk is convex in front and straight behind. The extremities are usually long, and the muscles are strongly developed. There are several sub-types of the Muscular, a Long and a Short, a Musculo-cerebral, a Musculo-respiratory, and a Musculo-digestive. The type makes up about 40 per cent of the population.

The *Cerebral type* appears in about 14 per cent of the people, and is the rarest of all the types, and represents the product of civilization. It occurs more often in late Egypt than in early Egypt (46). It is increasing in those places where civilization is advancing. The type is characterized by a small and slender body, a large and rounded head, remarkably developed upper face and reduced lower face. The frontal and parietal bosses of the cranium are well developed, the side view is spheroidal with a high auriculo-bregmatic diameter. The index is hyperbrachycephalic. The trunk is slender, the extremities short, the hands and feet small. There are mixed types as for the muscular.

The *Respiratory type* occurs in about 30 per cent of people. The middle part of the face is extremely well developed, the nose long, the maxillary bone large, the malar bones prominent, all the accessory sinuses of the nose including the mastoid are large. The eyes are far apart because of the large size of the nasal cavity, and the orbits are well separated. There is superior prognathism because of the large size of the maxillary bones. The face is lozenge-shaped because of its large size in the middle. The cranium is mesocephalic more than in the muscular type. The neck is long and well filled especially about the larynx which is large, with a prominent Adam's apple. The thorax is long and large, and the abdomen reduced by the size of the thorax,

which reaches nearly to the iliac crests. All the muscles of respiration are well developed, but those of the extremities are not. The persons are usually thin. The joints are not rough and prominent as in the muscular type nor are they small and graceful as in the digestive type. In the female they are specimens of grace and beauty, tall, delicately molded, with an oval face; they represent the Raphael and Leonardo de Vinci types. The Respiratory-cerebral types are common, but the Respiratory-digestive are rare and the Respiratory-muscular not uncommon.

The *Digestive type* is not common although present in about 20 per cent of the people. The outstanding characteristics are the large lower face, huge jaws and extremely ponderous abdomen. The mandible and zygoma are unusually well developed, and the teeth are large, regular and well formed. As age advances the double or triple chin becomes evident, fat accumulates about the buccinator muscles, the masticators, and the parotid gland about the ear, and this part of the face seems monstrous, and even raises the lobule of the ear and extends it forward. In spite of appearances the trunk is small. Its form is that of a cylinder slightly flattened in front and behind. A pad of fat covers it. The size of the abdomen reduces the size of the thorax considerably, making it short. The extremities are very long, the shoulders broad, the reach much greater than the stature. Mixed types are common, and the Digestive-muscular type is a veritable giant in some cases.

Bauer (5) follows the types of Sigaud and attempts to correlate their predisposition to diseases.

Other types have been added to these. Bach (2) (3) has shown a Wrestling type that appears distinctive after studying 85

measurements, indices and percentage relations of each person. This type is built like an inverted pyramid with a ball, the head, on top of the base. The shoulders are exceptionally broad, as is the thorax. The type is tall and heavy, and the muscles of the chest, arms, shoulders and neck are unusually well developed. The Digestive type, called Pykniker by the Germans, has also wide shoulders but compared with the Wrestler the difference is great. Thirty-three professional wrestlers, 95 amateur wrestlers, 3,457 German gymnasts, 710 students and 33 Pyknikers were compared. Taken in the above order the stature was found to be as follows: 177.3 cm., 169.1, 169.2, 172.5, and 167.9; the weight, 104.5 kg., 68.2, 64.5, 62.6, 73.9; the chest circumference, 117.4 cm., 98.7, 93.7, 88.2, 100.2; the abdominal circumference, 104.8 cm., 79.7, 76.1, . . . , 92.4; the shoulder breadth, 42.5 cm., 39.7, 38.9, 38.1, 38.3; the hip breadth, 34.5 cm., 29.4, 28.9, 28.8, 30.5; and the upper arm circumference, 37.2 cm., 30.5, 28.4.

Henckel (41) (42) tries to correlate Habitus, Constitution and Race, but finds considerable difficulty and little correlation. The Alpine and the Pykniker types correspond somewhat, the Nordic and the Leptoprosomic types are somewhat similar, and he includes the Cerebral and Respiratory under the latter but the Sanguine type and the Schizophrenic are minus and plus respectively in head measurements. The Nordic has head length and breadth and cephalic index extremely different from any other type. The curves of the measurements of the Pykniker and Sanguine types are parallel, as are also those of the Muscular and Schizophrenic. The Leptoprosomic are susceptible to tuberculosis and the muscular and digestive are susceptible to aortitis and kidney disease. The

Leptoprosomic including the Cerebral and Respiratory types are Hypermorphs, and the Muscular and Digestive are Mesomorph. The Pykniker and Manic-depressive types are related. Asthenic types should be called Leptoprosomic, or Linear, and they are the reverse of the Apoplectic according to Paulsen.

Viola (69) and Frassetto (33) Castaldi and Vannucci (23) follow the types as called Linear and Lateral by Stockard and Hypermorph and Mesomorph by Bean, to which they add a type between the others called the Normal returning to the same types that Manouvrier and Godin found. Frassetto still further divides the types into Microsplanchnic, Mesosplanchnic and Macrosplanchnic, under which he includes Microcephalic, Mesocephalic and Macrocephalic; and he still further subdivides these into Micromelic, Mesomelic and Macromelic, making 27 varieties in each of the three forms. Surely this does not exhaust the possibilities of type forms. They are much more numerous and their name is legion!

Mills (54b) has divided man into six types by the topography of the thorax and abdomen, hypersthenic (very stocky), hypersthenic-sthenic, sthenic, sthenic-hyposthenic, and hyposthenic (very long slender trunks). These may very readily be grouped into three by taking the two extremes, with all the others as intermediate.

Bardeen (4) has produced several masterly monographs on body build in relation to development, in which he concludes that judgment of build from height-weight index is greatly helped if we have some means of estimating relative length of lower extremities and relative adiposity. "Relative length of limbs may be most simply estimated from sitting-height as compared with stature. Relative adi-

posity may be most simply estimated from the relative circumference of the abdomen, or better from its relative antero-posterior diameter, since adiposity makes itself most clearly manifest here." He also concludes that the height-weight index is influenced by post-natal morphogenesis, sex, inherited individual or racial peculiarities, and peculiarities of structure due to habits of living or environment. Later he develops curves and formulae for working out the relative sitting height for comparison in different race, sex and age or other groups which may be of service in future race and type studies.

Davenport (28) from exhaustive studies of the inheritance of body build draws many interesting conclusions. The index of build is best expressed by the ratio of chest diameter to stature, or as that is rarely known, by chest circumference to stature. When only weight is known the best index is weight: (stature)³. The index is 2.52 for males and 2.43 for females. There are marked racial variations in build; there are also geographical differences; but the ontogenetic differences exceed these. The heavy build of the infant corresponds to that of the short-legged anthropoids, and the long-legged, slender build of the boy of 12 years persists in the Nilotic negroes and many low-grade feeble-minded. Changes in build vary with families. The polygon of mass numbers is skew in the direction of slenderness. Diseases of the slender build are tuberculosis, pneumonia, "nervousness," melancholia; of the fleshy build, diabetes, nephritis, dropsy, apoplexy, arterio-sclerosis, and paralysis following. Genetic build is controlled by multiple factors. Slender parents have slender children only, fleshy parents have both kinds. Hereditary factors probably work through the endocrine system. The number of factors involved in fleshy build

varies from 1 to 4 or more. The factors influence the functioning of the thyroid, pituitary and perhaps other glands.

Czckanowski (27) uses a four dimensional chart by which four characters may be shown graphically, and with this proceeds to clear up some of the types of Baden and Sweden. The Mediterranean type of Baden is not the small Ibero-insular, but the tall Atlanto-Mediterranean. Red hair is a variant of blond. The Alpine type in Sweden is taller than any other there except the Nordic. The Alpine type is associated with gray eyes and brown hair in Baden and in Sweden.

Pearl (58) has produced several books on human biology of great interest and importance, but his work is not directly related to human types. It would be well to know if the incidence of death from organic heart disease and the influenza death rate both occurred in the Mesomorph. Also it would be of interest to know why influenza and tuberculosis are not so intimately associated as the other two diseases, particularly as tuberculosis is prone to strike the Hypermorph. The death rates of Sao Paulo on the one hand,—mesodermal 3.8 and endo-epithelial 6.2,—and the United States, England and Wales on the other,—mesodermal 4.5 and endo-epithelial 10.0,—may be the result of a larger proportion of the Hypermorph in the Sao Paulo people who come largely from the Mediterranean stock.

Naccarati and Garrett have developed a "morphologic index" by dividing the length of one leg plus the length of one arm by the volume of the trunk. This gives skeletal extremity length and soft tissue volume as factors incompletely. They derive various conclusions as to temperament, intelligence, and physique from their results.

The whole question of physiologic

types hinges upon anatomic form, and this is inextricably bound up with race. With so many workers in the field there is hope of unravelling the threads.

V. SUMMARY

The evidence from human fossils in Europe points to the continuance of man there from the Mousterian period to the present day. Evidence from skeletal remains and from a study of living man indicates that the Black Race developed from the late Neanderthal forms that moved over from Europe into Africa and changed into the big Negro and the little Negrito; and that early "Australoid" forms moved eastward from Europe into southern Asia and the Pacific, followed by later forms of the Paleolithic and Neolithic periods, who came into Asia from the north and west. These continued from time to time over into America to produce the American Indian. Thus the Yellow-Brown race was formed.

There have been changes as the result of selection differing with locality. The interior continental peoples have remained somewhat like the original forms and are Mesomorph in type. The coast peoples have become smaller and slenderer and represent the Hypermorph. Under adverse living conditions the Hypomorph has evolved with a retention of the infantile condition.

It would seem that in Europe the Alpine is somewhat of a myth, the Nordic also and the Mediterranean. Likewise many variants under other names are more or less myths. A part of the population about the Baltic is tall, blond and long-headed, but many other forms are found about the Baltic and so it is about the Mediterranean and in interior continental Europe.

Many synonyms may be used to express about the same condition or type.

Broad-back, transverse, lateral, herbivorous, digestive, pykniker, muscular, apoplectic, plethoric, phlegmatic, lymphatic, Brachyskéle and Mesomorph mean about the same thing and so do narrow-back, linear, leptoprosomic, carnivorous, sanguine, respiratory, cerebral, nervous, phthisic, cachetic, choleric, Macroskéle and Hypermorph. The Mesomorph and Hypermorph mean more ontogenetically, phylogenetically and anatomically.

VI. GENERAL CONCLUSIONS

1. The types of the three great races of man have been classified chiefly by their ear form and nose type, but all other available characters have been utilized, especially the stature, sitting height and leg length.

2. Descriptions and illustrations have been given of the three types, Hypomorph, Mesomorph, and Hypermorph, although it is recognized that the descriptions fit only typical individuals. Other persons are more or less like one type or another. Variability is found in the form of blends, mixtures and mosaics.

3. The types are related in a general way to historic and prehistoric groups of men. The Whites are only of the Hypermorph and Mesomorph types; the Yellow-Browns are of the Hypermorph, Mesomorph and Hypomorph types; whereas the Blacks are only of the Mesomorph and Hypomorph types. The Blacks are in some ways more different from the remainder of mankind than are any other people. The most extreme anatomic forms of man are the Negrillo and the extreme form of Mediterranean Hypermorph.

4. Development seems to be from a more or less Hypomorph stage through the Mesomorph to the Hypermorph, whereas evolution seems to have been

from the massive Mesomorph to the extreme Hypermorph on the one hand and the extreme Hypomorph on the other. Evolution in the future is apt to come out of the three great masses of men, White, Black and Yellow-Brown, leaving aside small extraneous groups or fragments of mankind.

5. From previous studies (9) (11) (12) (13), it was shown that the *Epitheliopath* represents the abnormal Hypermorph and is susceptible to diseases of the structures derived from the embryonic ectoderm and entoderm, such as skin, nervous system and alimentary canal. They are also susceptible to chronic diseases such as tuberculosis of the lungs, cancer, pellagra, leprosy and other diseases of malnutrition. The *Mesodermopath* represents the abnormal Mesomorph and is susceptible to diseases of the tissues derived from embryonic mesoderm, such as heart and kidneys, arteries

and veins, joints and muscles. They are also susceptible to such acute diseases as pneumonia and typhoid fever. There is a question as to whether there are functional *epitheliopaths* and *mesodermopaths* or not. There may be changes in the soft tissues during the life of a person so that the diathesis may become, for instance, either plethoric or phthisic. The plethoric may resemble the Mesomorph and the phthisic may resemble the Hypomorph. Further studies should be made to determine whether the Mesomorph may become phthisic or the Hypermorph plethoric.

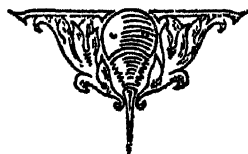
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LIST OF LITERATURE

- (1) ADAMS, F. *Airs, Waters and Places. The Genuine Works of Hippocrates*, I, 147-183, 1921.
- (2) BACH, F. *Körperbaustudien an Berufsringern*. *Anthrop. Anzeiger*, J. 1, H. 4, S. 200-212, 1924.
- (3) ——. *Brustumfang und Leibesübungen*. *Anthrop. Anzeiger*, J. 2, H. 3, S. 167-176.
- (4) BARDEN, C. R. The height-weight index of build in relation to linear and volumetric proportions and surface area of the body during post-natal development. *Contributions to Embryology*. Carnegie Inst. of Wash., v. 9, n. 46, 1919.
- (5) BAUER, J. *Beiträge zur klinischen Konstitutions pathologie. I. Habitus und Morbidität*. *Deutsch. Arch. f. klin. Med.* 125, 196, 1918.
- (6) BEAN, R. B. A series of articles on Filipino types, 245 pages in all, which appeared in the *Philippine Journal of Science* during the years 1908, 1909, and 1910.
- (7) ——. A series of articles on Filipino ear types, about 65 pages, many illustrations, in the same journal from 1908 to 1913.
- (8) ——. Types of Negritos in the Philippines. *Amer. Anthrop.* v. 12, p. 220-236. *Philippine Types*, *Ibid.*, p. 373-389, 1910.
- (9) ——. The Racial Anatomy of the Philippine Islanders. Lippincott, 1909.
- (10) ——. Some characteristics of the external ear. *Am. Jour. Anat.* v. 18, p. 291-325, 1916.
- (11) ——. Morbidity and morphology. *Johns Hopkins Hospital Bulletin*, v. 23, n. 262, Dec. 1912.
- (12) ——. Diseases and death rates in human types. *N. O. Med. and Surg. Jour.*, v. 69, p. 175-191, 1916.
- (13) ——. Die Morphologie und die Erkrankungen des Menschen. *Zeit. f. d. ges. Anat., Zeit. f. Konstitut.*, B. 9, H. 5, S. 439-450, 1924.
- (14) ——. The weights of the organs in relation to type, race, sex, stature and age. *Anat. Rec.*, v. 11, p. 326-328, 1917.
- (15) ——. Notes on the body form of man. *Eugenics in Race and State*, v. II, p. 7-24, 1923.
- (16) ——. The sitting height. *Amer. Jour. Phys. Anthrop.*, v. 5, n. 4, p. 349-390, 1922.

- (17) ———. The two European types. *Amer. Jour. Anat.*, v. 31, n. 4, p. 359-371, 1923.
- (18) ———. The three anatomic types of Africa. *Amer. Jour. Anat.*, v. 33, n. 1, p. 105-118, 1924.
- (19) ———. The types of the Yellow-Brown Race. *Amer. Jour. Anat.*, v. 35, n. 1, p. 63-80, 1925.
- (20) BOULE, M. *Les Hommes Fossiles*. Paris, 1925.
- (21) BRYANT, J. The carnivorous and herbivorous types of man. *Bost. Med. and Surg. Jour.*, v. 172, p. 321-324; v. 173, p. 384-387; v. 174, p. 412-416, 1915-1916.
- (22) ———. Physical types, dietary control and preventive medicine. *Conf. N. E. Ped. Soc. Bost.*, 1916.
- (23) CASTALDI, L., and VANNUCCI, D. Prima serie di osservazione anatomiche ponderali sulla grandezza di alcuni visceri nei tipi morfologici costituzionali col metodo del Viola. *Arch. di Biol. norm. e patol.* Fasc. 4-5, v. 78, 1924.
- (24) CHAILLOU, A. Considérations générales sur quatre types morphologiques humains. *Bull. et Mém. de la Soc. d'Anthrop. de Paris*, 6 sér., v. 1, n. 3, f. 3, p. 141-150, 1910.
- (25) CHAILLOU, A., and MAC-AULIFFE, L. Le type musculaire. *Bull.*, etc., p. 201-224, 1910.
- , and MARIE, A. Le type cérébral. *Ibid.*, p. 311-322, 1910.
- , Le type respiratoire. *Ibid.*, p. 344-358, 1910.
- , Le type digestive. *Ibid.*, p. 597-607, 1910.
- (26) CROOKSHANK, F. G. *The Mongol in Our Midst*. Dutton, 1924.
- (27) CZEKANOWSKI, J. Le problème de la synthèse des cartogrammes et les types anthropologique. *Anthropologie*, v. 2, n. 3-4, p. 151-164, 1924.
- (28) DAVENPORT, C. B. *Body-Build and Its Inheritance*. *Carneg. Inst. Wash. Pub.*, n. 329, 1923.
- (29a) DENIKER, J. *The Races of Man*. Scribner's, 1906.
- (29b) DE QUATREFAGES, A. *Histoire Générale des Races Humaines*. Paris, 1889.
- (30) DIXON, R. B. *The Racial History of Man*. Scribner's, 1923.
- (31) DRAPER, G. *Human Constitution. A Consideration of Its Relationship to Disease*. Philadelphia and London, 1924.
- (32) FLEURBAEY, H. F. *The Races of England and Wales*, 1922.
- (33) FRASSETTO, F. Il numero e la varietà dei tipi costituzionali e delle combinazioni morfologiche individuali in antropologia e in medicina. *Riv. di Biologia*, v. 4, f. 3, 1922.
- (34) GODIN, P. Les proportions du corps pendant la croissance. *Bull. et Mém. de la Soc. d'Anth. de Paris*, 1910.
- (35) GOLDTRWALT, J. E. An anatomical and mechanistic conception of disease. *Bost. Med. and Surg.*, v. 172, p. 881-896, 1915, v. 174, p. 160-161, 1916.
- (36) GORJANOVIC-KRAMBERGER, K. *Der diluviale Mensch von Krapina*, 1906.
- (37) GREMIATZKY, M. A. La calotte du crâne de l'homme de Podkournak. *Anthropologie*, Cisko 2, p. 164-166, 1923.
- (38) GÜNTHER, H. F. K. *Rassenkunde des Deutschen Volkes*. Lehman, München, 1923.
- (39) HADDON, A. C. *The Races of Man and Their Distribution*, Macmillan, 1925.
- (40) HARRINGTON, SIR J. *The School of Salernum*. The English Version, 1920.
- (41) HENKEL, K. O. Körperbaustudien an Geisteskranken, III, Konstitutioneller Habitus und Rassenzugehörigkeit. *Zeitsch. f. d. gesamt. Neurol. u. Psych.*, B. 43, H. 1-2, 1924.
- (42) ———. Die Korrelation von Habitus und Erkrankung. *Berlin. Klinische Wochen.*, 3 J., n. 37, p. 1670-1671, 1924.
- (43) HOOTON, E. A. The asymmetrical character of evolution. *Am. J. Phys. Anthropol.*, v. 8, n. 2, 1925.
- (44) ———. Methods of racial analysis. *Science*, v. 43, p. 75-81, 1926.
- (45) HUTCHINSON, J. *The Pedigree of Disease, Temperament, Idiosyncrasy and Diathesis*. 1884.
- (46) HRDLIČKA, A. The natives of Kharga Oasis, Egypt. *Smithsonian Misc. Coll.*, v. 59, n. 1, 109 pages, 1922.
- (47) ———. The most ancient skeletal remains of man. *Smithsonian Reports*, p. 491-552, 1914.
- (48) ———. The peopling of Asia. *Proc. Am. Phil. Soc.*, v. 4, p. 535-545, 1921.
- (49) ———. *The Old Americans*. Williams and Wilkins, Baltimore, 1925.
- (50) LOVEDAY, T., and FORSTER, E. F. *Physiognomica, The Genuine Works of Aristotle*, I, 805a-814b, 1913.
- (51) MACCURDY, G. G. *Human Origins*. Appleton, 1924.
- (52) MATIEGKA, J. Lebka podbabská. *Anthropologie*, v. 2, n. 1, p. 1-16, 1924. Crâne de Podbaba (Bohême) (Résumé).
- (53) MAWER, A. *The Vikings*. Cambridge, 1913.

- (54a) MANOUVRIER, L. Étude sur les rapports anthropométrique en générale et sur les principales proportions du corps. *Mém. de la Soc. d'Anth. de Paris*, ser. 3, 2, 1902.
- (54b) MILLS, W. W. The relation of bodily habitus to visceral form, position, tonus and motility. *Am. J. of Roentgenology*, v. 4, p. 155, 1917.
- (55) MONTELIUS, O. The Immigration of Our Forefathers to the North. The Swedish Nation in Word and Picture, Stockholm, 1921.
- (56) OSBORN, H. F. Men of the Old Stone Age. Scribner's, 1915.
- (57) PRAKE, H. The Bronze Age and the Celtic World. Benn Bros., London, 1922.
- (58) PEARL, R. Studies in Human Biology. Williams and Wilkins, Baltimore, 1924.
- (59) RIPLEY, W. Z. The Races of Europe. Sec. Ed., London, 1912.
- (60) SCHULTZ, A. H. Embryological evidence of the evolution of man. *Jour. Wash. Acad. Sc.*, v. 15, n. 12, 1925.
- (61) SERGI, G. The Mediterranean Race. London, 1906.
- (62) SIGAUD, —. *Traité clinique de la digestion et du régime alimentaire*. Paris, Doin, 1908.
- (63) SMYČKA, J. Découverte de squelettes d'homme dans les sédiments quarternaires, á Mladeč (Moravie). *Anthropologie*, v. 2, p. 166-170, 1923.
- (64) STEENSBY, H. P. Preliminary observations on the racial types in Denmark. *Forelobige Betragtninger over Danmarks Raceantropologi. Meddelelser om Danmarks Antropologi udgivne af den antropologiske komité*, I Band, Kobenhavn, 1907-1911.
- (65) STRATZ, C. H. *Naturgeschichte des Menschen*. Stuttgart, 1904.
- (66) STOCKARD, C. R. Human types and growth reactions. *Am. Jour. Anat.*, v. 31, n. 3, p. 261-288, 1923.
- (67) TREVBS, SIR F. *British Medical Journal*, v. 1, p. 583, 1886.
- (68) TRICOLET. *Essai sur la forme du corps humain*. Thèse. Lyon, 1908.
- (69) VIOLA, G. Il metodo antropometrico di "deformazioni" per la classificazione clinica dei tipi morfologici. In A. DeGiovanni "Lavori del Instituto di Clinica Medica di Padova," p. 56, Milano, Koepli, 1908-1909.
- (70) VERNEAU, R. La race de Neanderthal et la race Grimaldi; leur role dans l'humanité. (The Huxley Memorial Lecture for 1924.) *The Jour. Roy. Anthropol. Soc. Gr. Brit. and Ireland*, v. 54, p. 211-230, 1924.





THE BIOLOGY OF HOST-PARASITE RELATIONSHIPS AMONG PROTOZOA LIVING IN MAN

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I. INTRODUCTION

PARASITOLOGY is a subject of interest to students of various branches of biology. It is taught in the zoology departments of many colleges and universities and in medical schools, especially in schools of tropical medicine. Investigations in this field are carried on principally by zoologists and medical men. Zoologists who are interested in parasitology usually direct their attention primarily to the parasite, whereas most medical men tend to emphasize the reactions of the host. The zoological parasitologist, for the most part, is concerned with morphology, systematics, and life-history studies, and the medical parasitologist with symptomatology, pathology and therapeutics. Only when these two phases of the subject are brought together and when the aspects of the subject peculiar to public health activities are added is a complete program realized; then parasitology becomes the Biology of Host-Parasite Relationships.

The following discussion of the biology of host-parasite relationships is limited to the parasitic protozoa because that is the group of disease-producing organisms with which the writer is most familiar. Probably every species of animal serves as a host to one or more species of protozoa peculiar to itself and these are so varied in their host-parasite relationships that it becomes necessary to further limit

our program to a small group of parasites that live in one species of host—man—referring where it seems advisable to related species in lower animals. The relations of the spirochetes to the bacteria and protozoa are still obscure; consideration of the spirochetes is, therefore, omitted here.

One who studies protozoa soon comes to realize that there is no essential difference between free-living species and parasitic species; both types must maintain themselves in their environment and must provide by reproduction for the maintenance of the race. Species living on or within other animals or plants usually exist among relatively more limited and stable surroundings and are more rigidly adapted to one type of environment than are free-living species. Both parasite and host, however, are variable and must be adjusted to each other, thus offering opportunities for the study of the reciprocal influences of organisms. Furthermore, parasites and hosts may, in many cases, be separated and studied apart from each other; this involves experimental procedure without which progress along the lines suggested in our program becomes impossible.

Those who have not interested themselves particularly in parasitology may not be familiar with some of the terms in common use; to these the following definitions may be of value. It is perhaps desirable first to distinguish between parasitism and predatism. A parasite

is an organism that lives on or in and at the expense of another organism without immediately destroying it. A predaceous animal also lives at the expense of other animals but kills them directly and devours them. There are in nature a continuous series of intermediate stages between parasitism on the one hand and predatism on the other.

The term symbiosis was proposed by deBary in 1879 for the constant, intimate and mutually beneficial association of two organisms. Etymologically, symbiosis means simply "living together" and hence should include parasitism, mutualism, commensalism and all other types of consociation, but the term now implies the permanent association of two specifically distinct organisms so dependent on each other that life apart is impossible. When the association is less intimate but each partner benefits the other the term mutualism is sometimes employed. The terms commensalism and inquilinism are often used for still looser associations. Commensalism is applied to the regular association of two definite species of organisms which "eat together at the same table" but not at each other's expense. Very similar in meaning is inquilinism, which is used to describe the condition where one animal lives with another as a cotenant but usually not at its expense.

The origin of these various types of association is, of course, not definitely known, but can be inferred without much difficulty because of the existence of a large number of intermediate stages.

That they have arisen many times is indicated by their wide distribution among the phyla in the animal kingdom. The evolution of parasitism is one of the most interesting of all biological problems and, as has been pointed out by several writers, parasites offer particularly favorable material for the study of the course of evolution, since parasites undoubtedly originated from free-living organisms from which they have become differentiated by a sort of superimposed evolution, and in many cases the free-living ancestors of these parasites still exist.

One very striking effect of the parasitic habit is that generally called degradation. This term implies that the parasite has degenerated, but although some of the parts of the parasite undergo degeneration, others become more highly developed. It seems better therefore to speak of the parasitic condition as a specialization rather than a degradation or regression, especially since most parasites are marvelously adapted to their mode of life.

II. PROTOZOA LIVING IN MAN

Each of the four classes of the protozoa includes species that live in man; these are represented by drawings on Plates 1 to 3 and referred to by number below. To the Class Sarcodina belong six species of amoebae, *Endamoeba gingivalis* (fig. 5) in the mouth, and *Endamoeba coli* (figs. 2a, 2b), *Endamoeba histolytica* (figs. 1a, 1b), *Endolimax nana* (figs. 3a, 3b), *Iodamoeba williamsi* (figs. 4a, 4b), and *Dientamoeba fragilis* (fig. 6) in the large intestine.

PLATE 1

AMOEBAE LIVING IN MAN

(All figures magnified about 2000 diameters.)

1a and 1b. *Endamoeba histolytica*. 1a, trophozoite. 1b, cyst. (After Dobell.)

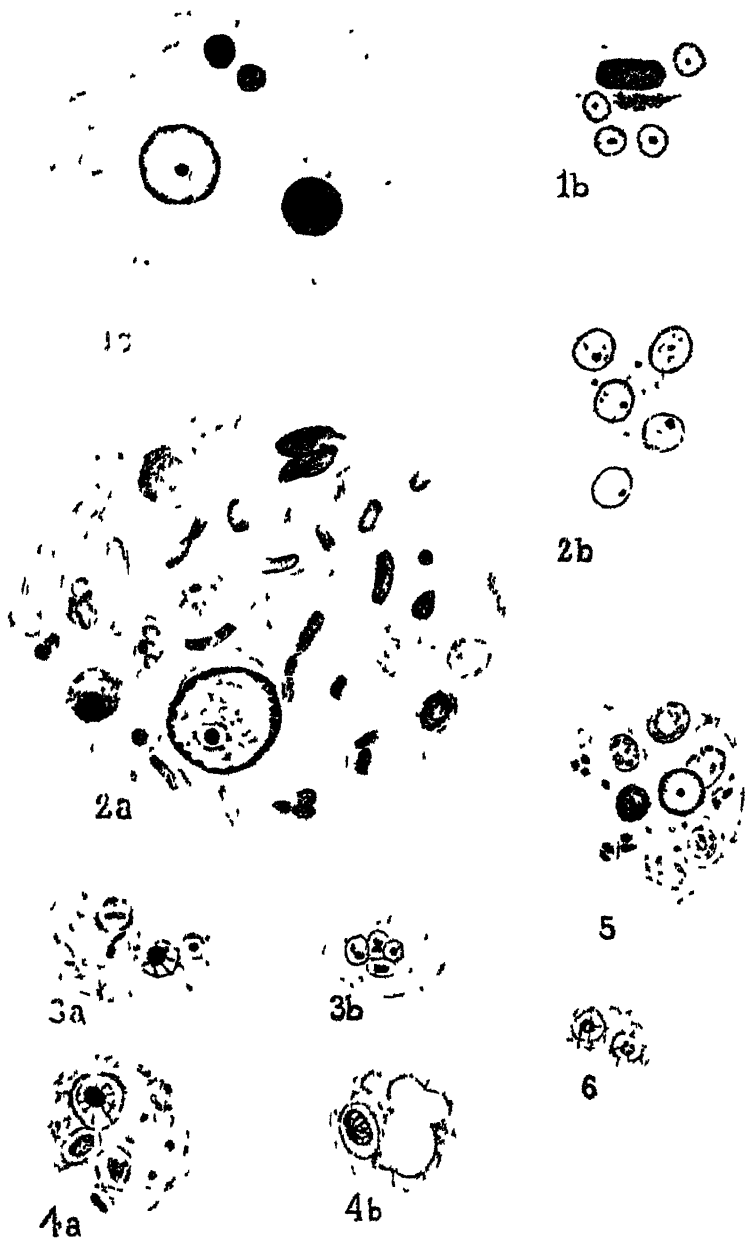
2a and 2b. *Endamoeba coli*. 2a, trophozoite. 2b, cyst. (After Dobell.)

3a and 3b. *Endolimax nana*. 3a, trophozoite. 3b, cyst. (After Taliaferro and Becker.)

4a and 4b. *Iodamoeba williamsi*. 4a, trophozoite. 4b, cyst. (After Taliaferro and Becker.)

5. *Endamoeba gingivalis*. (After Dobell.)

6. *Dientamoeba fragilis*. (After Taliaferro and Becker.)



The Class Mastigophora contains two groups, six species of hemoflagellates and eight species of intestinal flagellates. The hemoflagellates are *Trypanosoma gambiense* (fig. 18) and *T. rhodesiense* (fig. 19), the organisms of African sleeping sickness; *T. cruzi* (fig. 20), that causes Chagas' disease of South America; *Leishmania donovani* (fig. 21), the organism of kala-azar; *L. tropica* (fig. 22), the etiological agent of oriental sore; and *L. americana* (fig. 23), the causative agent of uta or American leishmaniosis in South America. The so-called intestinal flagellates include *Giardia lamblia* (figs. 13a, 13b), an inhabitant of the duodenum; *Chilomastix mesnili* (figs. 10a, 10b), *Embodonas intestinalis* (figs. 11a, 11b), *Tricomonas intestinalis* (figs. 12a, 12b), *Enteromonas hominis* (fig. 14), *Trichomonas hominis* (fig. 9), which live in the large intestine; *Trichomonas buccalis* (fig. 8), an inhabitant of the mouth; and *T. vaginalis* (fig. 7) which occurs in the vagina.

The Class Sporozoa is represented by three species of coccidia, *Isospora hominis* (fig. 15), *Eimeria wenyoni* (fig. 16), and *E. oxyuris* (fig. 17), which penetrate into the intestinal epithelium (there is some doubt regarding the validity of the last two species); three species of malarial parasites, *Plasmodium vivax* (fig. 26a, b, c), the organism of tertian malaria, *P. malariae* (fig. 27a, b, c), of quartan malaria, and *P. falciparum* (fig. 28a, b, c), of estivo-autumnal malaria, all of which invade red blood corpuscles; and one species of muscle parasite of the genus *Sarcocystis* (fig. 25).

Only one species of the Class Infusoria is known with absolute certainty to be a parasite of man; this is the ciliate *Balantidium coli* (fig. 24), which lives in the large intestine and gives rise sometimes to balantidial dysentery. Besides these eight groups, which are recognized by all

protozoologists, there is a long list of protozoa that have been described from man about the authenticity of which there is still some doubt.

Each species of protozoon is rather definitely limited to a certain region of the body—organ or tissue. How this localization is brought about can only be conjectured. It may be noted, however, that in most cases the parasites live where their offspring can easily escape from the host or where they are likely to be ingested by intermediate hosts. Most of the species enumerated above live in the digestive tract; this is true of all of the amoebae, coccidia, and intestinal flagellates and of *Balantidium coli*; nine species are blood-inhabiting hemoflagellates and hemosporidia; one species occurs in the vagina and one in muscle. The species of the genus *Sarcocystis* that have been reported rarely in the muscle of man are probably accidental parasites that, through some peculiar circumstances, are rarely able to initiate an infection; but no chance exists of their offspring escaping from the host.

III. EPIDEMIOLOGY OF TRANSMISSION

1. Infective stage

Perhaps the most satisfactory point at which to begin the study of the biology of host-parasite relationships is the infective stage of the parasite. The organisms during the period of the infective stage may be well protected by the host, as in malaria, in which case the infective sporozoites are inoculated directly into the blood of man by a mosquito, but usually are subjected to various environmental factors from the time they escape from the body until they gain entrance into a new host. The idea maintained by many of the older authorities that disease-producing organisms may multi-

ply outside of the host and bring about foci of infection in soil or water has been abandoned since it has been abundantly proved that very little if any increase in numbers occurs under these conditions.

The malarial organism, for example, which was at one time supposed to pass part of its existence in the waters of ponds and streams is now known to lack a free-living existence entirely. The environment of the intermediate host, however, has an influence on the development of the infective sporozoites of the malarial plasmodium since the organism in the mosquito does not continue normal growth and differentiation if the temperature is too low or too high and each species of malarial organism has its own optimum temperature. Similar factors are also involved in the life-cycles of blood-inhabiting protozoa that are insect borne.

Unlike the hematozoa, which are comparatively few in number, most of the disease-producing protozoa of man escape from the body in a cyst-like condition and spend part of their life-cycle outside of the host. The problems encountered during this period are extremely serious and very few of the organisms survive the vicissitudes of a free-living existence. The two principal problems encountered by the parasites are (1) that of withstanding the factors in their new

environment and (2) that of developing to the infective stage. The first problem is particularly difficult for protozoa such as the intestinal flagellate, *Trichomonas hominis* (fig. 9), that do not form resistant cysts but pass from one host to another in the active, trophozoite stage. These trophozoites can exist only in a liquid medium and are presumably very susceptible to modifications of temperature, to chemical changes in the environment and to mechanical injury. Most protozoa, however, are protected by one or more resistant walls secreted by the organism, which help prevent loss of water; keep out injurious substances; and guard against molar agents. The terms applied to these resistant bodies are "cyst" (fig. 1b) in the case of intestinal amoebae, flagellates and ciliates, and "oöcyst" (fig. 15) in the coccidia.

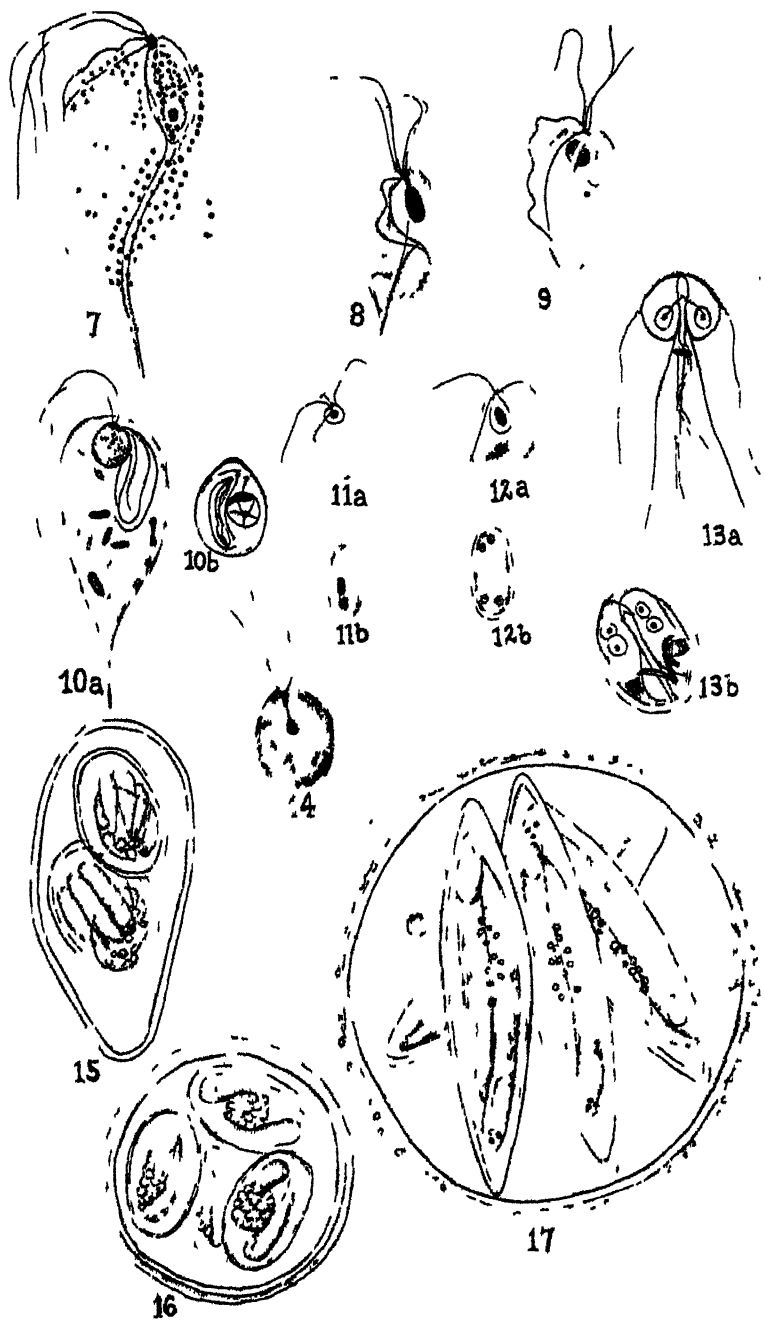
In most cases, probably no development occurs within the cysts after they escape from the body. Thus in the dysentery amoeba, *Endamoeba histolytica*, cysts with from one to four nuclei (fig. 1b) pass out with the feces, but the uninuclear and binuclear immature cysts do not develop further and die more quickly than do the quadrinucleate, mature cysts (Dobell, 1919). The oöcysts of coccidia, on the other hand, continue their development if discharged when still immature. The oöcyst of the most common human

PLATE 2

FLAGELLATES (FIGS 7 TO 14) AND COCCIDIA (FIGS 15 TO 17) LIVING IN MAN

(All figures of flagellates magnified about 2000 diameters and of coccidia about 1600 diameters.)

7. *Trichomonas vaginalis*. (After Hegner)
8. *Trichomonas buccalis*. (After Goodey and Wellings)
9. *Trichomonas hominis*. (After Faust.)
- 10a and 10b. *Chlamydomonas muris*. 10a, trophozoite. 10b, cyst. (10a, after Boeck, 10b, after Kofoid and Swazy)
- 11a and 11b. *Embadomonas intestinalis*. 11a, trophozoite. 11b, cyst. (After Hegner)
- 12a and 12b. *Tricercomonas intestinalis*. 12a, trophozoite. 12b, cyst. (After Wenyon and O'Connor.)
- 13a and 13b. *Giardia lamblia*. 13a, trophozoite. 13b, cyst. (After Simon)
14. *Enteromonas hominis*. (After Fonseca)
15. *Isospora hominis*. (After Dobell.)
16. *Eimeria wenyon*. (After Wenyon.)
17. *Eimeria oxyuris*. (After Dobell.)



species, *Isospora hominis*, is still in a unicellular condition when it escapes from the body. Its protoplasm then divides into two sporoblasts which become spores by secreting resistant walls about themselves. Four sporozoites are then formed within each spore (fig. 15) (Wenyon, 1915). Presumably not until these sporozoites are fully developed does the oöcyst become infective.

It seems clear from the evidence available (1) that no foci of infection of disease-producing protozoa exist outside of the host and (2) that in the majority of cases certain stages are already infective when they escape from the body and all other stages including trophozoites and immature cysts die outside of the host.

2. Avenues of infection

Reaching and invading a new host is perhaps the most serious problem in the entire life-cycle of a parasitic protozoon so far as the maintenance of the species is concerned. Only the smallest fraction of the total number of infective organisms can possibly reach a susceptible animal in which to live, and only the almost inconceivable fecundity of the parasites prevents the various species from dying out. In the most simple cases the infective stage of the parasite is ingested with the food or drink of the proper host. The parasite is passively carried in the medium by which it is surrounded and it is the behavior of the host that leads to invasion. This is the contaminative method of parasite transmission. Laboratory experiments, mostly with lower animals, have established this as an effective method and there is no other obvious way in which infective cysts in nature can obtain entrance to the host.

Cysts remain alive only a few days in undiluted feces, but may live for a considerable period when kept in water.

Thus Boeck (1921) found that washed cysts of the intestinal flagellate, *Giardia lamblia* (fig. 13b), lived over two months and those of *Chilomastix mesnili* (fig. 10b) over seven months. These cysts as well as those of certain intestinal amoebae are able to withstand temperatures considerably higher than those normally encountered in nature. The problem of the parasite is to reach the mouth of the host before death results from drying, bacterial action, or starvation within the cyst. A moist warm climate is therefore favorable for transmission. Unsanitary conditions due to neglect on the part of the host are also favorable since this leads to the pollution of drinking water, milk and other food substances. Flies probably play an important rôle in the distribution of the cysts of intestinal protozoa. Root (1921) and others have shown that these cysts may remain alive for a considerable period within the intestine of the fly, e.g., those of *Giardia lamblia* (fig. 13b) at least 24 hours, and may be deposited in a living condition as early as 40 minutes after the fly has fed on contaminated material. In general it may be said that transmission by the contaminative method is more easily effected in rural than in urban communities, and in the tropics than in the temperate regions.

There are three other principal methods of reaching a new host. These are (1) by "contagion" or direct transference from definitive host to definitive host, (2) by inoculation through the agency of an intermediate host, and (3) by "inheritance." The "hereditary" method of transmission does not occur so far as I know in any protozoon living in man; but takes place in a number of parasites of lower animals. For example, the microsporidion, *Nosema bombycis*, that causes *pébrine* in France and *gattina* in Italy, invades the eggs within the ovaries as

well as other tissues of infected silkworms and the spores germinate in the larvae that hatch from these eggs; the young silkworms thus "inherit" the infection. In a similar manner the hemosporidion, *Piroplasma bigemina*, that causes Texas fever in cattle, is transmitted from the intermediate host, usually a tick of the genus *Boophilus*, to its offspring through the egg.

The direct or contagious method of transmission may be brought about in various ways. Among human protozoa the amoeba, *Endamoeba gingivalis* (fig. 5) and the flagellate, *Trichomonas buccalis* (fig. 8), that live in the mouth, no doubt are transferred directly from one host to another by kissing. The flagellate, *Trichomonas vaginalis* (fig. 7), which is apparently widespread among women and has been recorded from the urinary tract of man, is probably distributed during coitus. The high incidence of infection by these flagellates is not generally realized. *Trichomonas vaginalis*, for example, was found by the writer (Hegner, 1925) in vaginal smears from exactly 50 per cent of the women examined at hospitals in Honduras and Costa Rica in the summer of 1924. These organisms might almost be considered ectoparasites since they do not penetrate into the body tis-

sues. Among the lower animals direct contact is responsible for the transmission of certain endoparasites; for example, the hemoflagellate, *Trypanosoma equiperdum*, which lives in the blood of horses in various parts of the world and causes a disease known as dourine is transferred from one host to another through the mucous membranes during coitus.

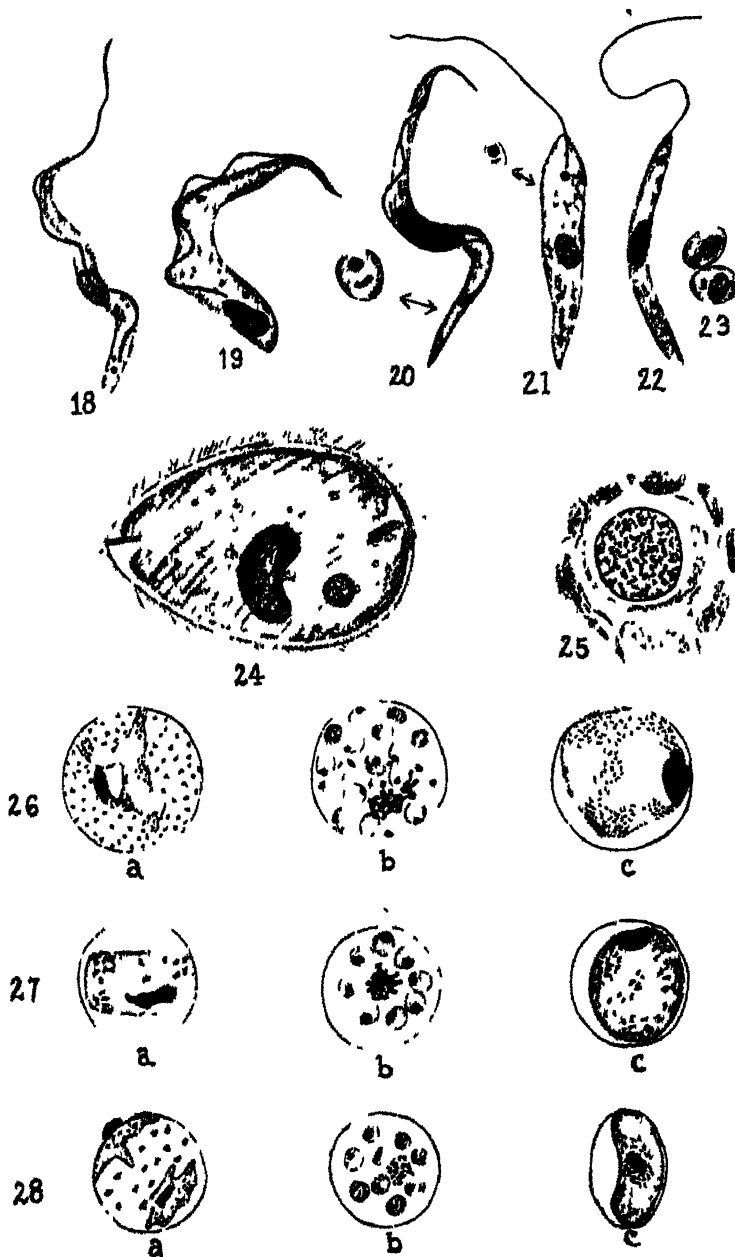
Inoculation by an intermediate host is a very common method of transmission and involves the most complicated behavior on the part of host, intermediate host and parasite. In malaria, for example, only the females of certain species of mosquitoes become infected; these must suck up the blood of malaria patients and do not usually become infected unless this blood contains at least twelve sexual parasites (gametocytes) per cubic millimeter; the external temperature must not go beyond certain limits, as noted above, or the life-cycle within the mosquito is not completed; the mosquito must protect itself from numerous dangers in its environment for from 8 to 18 days depending on the temperature and species of parasite before the infective stage, the sporozoite, is reached; then if a susceptible host chances to be abroad after dusk or at dawn or is unprotected by netting during the night and an infective

PLATE 3

HEMOFLAGELLATES AND SPOROZOA LIVING IN MAN

(All magnified about 2000 diameters except no. 24, about 700, and no. 25 magnification unknown.)

18. *Trypanosoma gambiense*. (After Hegner and Taliaferro.)
19. *Trypanosoma rhodesiense*. (After Hegner and Taliaferro.)
20. *Trypanosoma cruzi*; flagellate stage and leishmania stage. (After Hegner and Taliaferro.)
21. *Leishmania donovani*; flagellate stage and leishmania stage. (After Hegner and Taliaferro.)
22. *Leishmania tropica*, flagellate stage. (After Row.)
23. *Leishmania americana*; leishmania stage. (After Row.)
24. *Balantidium coli*. (After Hegner and Taliaferro.)
25. *Sarcocystis*. (After Baraban and Saint-Remy.)
- 26 to 28. Malaria parasites within human red blood corpuscles.
26. *Plasmodium vivax* of tertian malaria. *a*, schizont; *b*, merozoite formation; *c*, gametocyte. (After Hegner, Cort and Root.)
27. *Plasmodium malariae* of quartan malaria. *a*, schizont, *b*, merozoite formation; *c*, gametocyte. (After Hegner, Cort and Root.)
28. *Plasmodium falciparum* of aestivo-autumnal malaria. *a*, schizont; *b*, merozoite formation; *c*, gametocyte. (After Hegner, Cort and Root.)



mosquito chances to encounter him, sporozoites are inoculated during the three or four minutes occupied by the mosquito in getting a meal of blood. The conditions of successful transmission in this case seem so complicated that it is surprising that malaria can continue to exist; nevertheless it is today economically the most important of all diseases in tropical and semitropical countries.

Other human diseases, the protozoan organisms of which are transmitted by inoculation, are African sleeping sickness, due to trypanosome flagellates (figs. 18, 19) and spread by tsetse flies; Chagas' disease of South America, due also to trypanosome flagellates (fig. 20) and carried by bugs of the genus *Triatoma*, and possibly kala-azar (fig. 21) and other leishmanioses, the method of transmission of which is still unknown. Many of the protozoan parasites of lower animals are also transmitted by the inoculative method, the relations of host and parasite in each case being usually as complicated as in human malaria and of almost infinite variety.

IV. HOST-PARASITE RELATIONSHIPS DURING A NATURAL INFECTION

The term natural infection is used here to designate an infection in nature during which the parasite is able to pass through its life-cycle successfully and provide infective stages for the invasion of a new host or intermediate host. In contrast to natural infections, are conditions that result from the invasion of hosts that may be called foreign, refractory, accidental or casual,—terms that are fully explained below under the subheading Host-Parasite Specificity.

1. The course of infection

a. Parasitological periods (see text figure).

(a) The *Prepatent Period* extends from the

time the infective parasites enter the body of the host until their offspring can be recovered by the usual laboratory methods. The length of this period obviously depends to some extent on the character of the laboratory technique employed.

(b) The *Patent Period* covers the interval during which the parasites can be demonstrated by microscopical technique. The parasite number undergoes a *Rise* during this period, reaches a *Peak* and then suffers a *Fall*. The patent period ends when the parasites can no longer be found in the blood, feces, etc.

(c) In many infections the patent period is followed by a *Subpatent Period* of indefinite length. During this period parasites can not be recovered by the usual laboratory methods but their presence can be proved in various ways depending on the species of parasite. For example, protozoan cysts may disappear from the stools but reappear after a few days, weeks or months have elapsed; and malarial parasites may no longer be demonstrable in the blood of a host but may again become evident during a subsequent relapse. In bird malaria the subpatent period may extend over several years, i.e., from the end of the acute attack until the death of the bird; during all this time parasites cannot be found in the blood by the usual technique, but their presence can be demonstrated by inoculating some of the blood into a fresh bird, in which an acute attack develops.

The subpatent period may be followed by a second patent period during which the parasite number rises, reaches a peak, and falls but often does not rise as high as in the primary attack.

b. Clinical periods (see text figure).

(a) The *Incubation Period* extends from the time of the entrance of the parasites until symptoms appear. This period is usually

longer than the prepatent period, but may be shorter. For example, in cats infected with the coccidion, *Isospora felis*, diarrhetic symptoms appear before oöcysts are recoverable in the feces. As indicated in the text figure the number of parasites usually increases considerably before symptoms become evident. The curves as given probably do not represent actual conditions in any specific protozoan infection but are meant to indicate that

symptoms disappear, but later with the recovery of the host.

(d) In diseases characterized by relapses one or more *Latent Periods* may be present. During these periods the causative organisms are too few in number to bring about symptoms, but after intervals of indefinite length, some change occurs in parasite or host or in both that results in an increase in parasite number and a reappearance of symptoms.

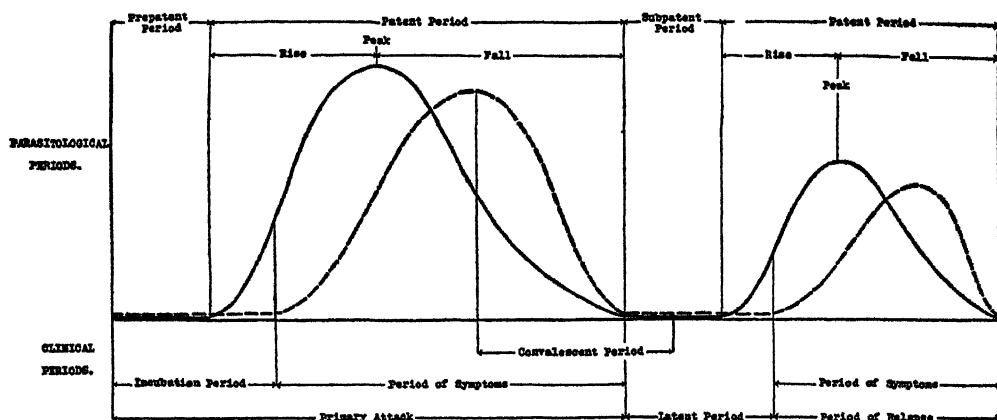


FIG. 1

This illustration is intended to represent by means of curves the parasitological and clinical periods in the course of infections with pathogenic protozoa. It represents in a general diagrammatic way the course of natural infections, consisting of a primary attack followed by apparent recovery of the host. This completes both the parasitological and clinical manifestations of disease in cases such as oriental sore in which one attack gives immunity. In other diseases, however, such as amoebic dysentery and malaria, the primary attack is often followed by a symptomless period when the parasites are latent. Eventually the parasite number again increases, symptoms reappear and the host is said to suffer a relapse. The terms used are fully described in the text.

(I am indebted to the members of my Seminary in Protozoology and especially to Dr. Justin M. Andrews for various suggestions in preparing this diagram.)

in general the increase in parasite number precedes the appearance of symptoms and that increases and decreases in the severity of the symptoms follow the rise and fall in parasite number.

(b) The *Period of Symptoms* begins when the incubation period ends and ends of course with the cessation of symptoms.

(c) The *Convalescent Period* is represented as beginning at the point of maximum symptoms. It ends, not when the

(e) The reappearance of symptoms following a latent period is known as the *Period of Relapse*.

2. Distribution and localization of parasites within the host

a. *Distribution*. As already noted protozoan parasites may gain entrance to their natural hosts by way of the mouth in contaminated food or drink, by direct contact, by inoculation through an inter-

mediate host and by "inheritance." The distribution of the protozoa after they enter the body is at first due almost entirely to the activities of the host and is determined by the point and method of entrance. Blood-inhabiting species, such as malarial organisms and trypanosomes, are rapidly carried to all parts of the body in the blood stream; intestinal-inhabiting species are transported with the food through the esophagus and stomach and into the intestine. Species that are transmitted by contact remain usually in the region of entrance, e.g., in the mouth or genital cavities.

b. Primary site of infection. Different species of protozoan parasites become localized in different organs, tissues or cells of the body depending on various factors. Certain parts of the body are more frequently affected than others, e.g., the blood and intestine, a fact that is probably vitally associated with the necessity of the offspring to escape from the host. The parasites may be (1) coelozoic, i.e., localized in cavities, such as the digestive tract, coelom or body cavity, blood or lymph spaces, and genito-urinary cavities, or (2) histozoic, i.e., within the tissues, where they may live among the cells (intercellular), within the cells (intracellular or cytozoic), and even within the nuclei (intranuclear). The factors that are responsible for localization are not well known. The parasites are subjected to various conditions in their environment just as free-living protozoa are in theirs; they must protect themselves from injurious agents, such as secretions and excretions; must reach a location where the proper nutriment is available; must possess some means of fixing themselves in a favorable situation; and must be able to carry on reproductive processes.

Certain intestinal flagellates of man

are of particular interest for purposes of illustration (Hegner, 1923). The optimum habitat of *Giardia lamblia* (fig. 13a) seems to be the lumen of the duodenum whereas that of *Trichomonas hominis* (fig. 9) is the lumen of the large intestine. The contents of the duodenum are mostly sterile and consist of products of digestion that pass through from the stomach to the jejunum and of various secretions from the stomach, liver, pancreas and intestinal wall. *Giardia* has no mouth and does not ingest solid particles of food and, so far as is known, does not destroy the tissues of the host; its nutriment is absorbed through the surface of the body. Just what part of the material by which it is surrounded is utilized has not been determined. All inhabitants of the small intestine must maintain their positions against the action of peristalsis. *Giardia* is able to do this because of the presence of a sucker-like disc with which it fastens itself to the surface of the epithelial cells. Spaces among the intestinal villi are also of value since they furnish a haven where downward currents are less pronounced. *Trichomonas*, on the other hand, never occurs in the duodenum, unless it is just passing through, and is seldom encountered in the jejunum or ileum; its favorite habitat is the large intestine and especially the cecum. Experiments carried on by the writer with the trichomonads of rats (Hegner, 1925) indicate that these flagellates, as well as the species (*Trichomonas hominis*) that occurs in man, infect new hosts in the active, trophozoite stage and are carried through the mouth, esophagus, stomach and small intestine and into the large intestine unharmed and still able to set up a new infection. Thus when rats were fed milk containing active specimens and killed and examined within from one-half hour to two hours later, it was found in one case that the flagellates

had passed through 780 mm. of intestine and had reached the cecum within one-half an hour. The experiments indicated that the trichomonads are unable to maintain themselves against the action of peristalsis but are carried directly to the large intestine; here they find conditions such that they are able to swim against the slow movement of material toward the outside, especially when they get into the eddy-like contents of the cecum. There is some evidence that movement of the trichomonads is partially inhibited in the stomach and anterior portion of the small intestine, but regained as the large intestine is approached. In the large intestine nutritive conditions are favorable since *Trichomonas* has a mouth and may ingest solid food particles which are present there in abundance.

Localization among tissue parasites offers many problems that are still unsolved. What factors influence the sporozoites of malaria to attack the red blood cells, and those of the coccidia to attack the epithelial cells of the intestine? What causes *Endamoeba histolytica* (fig. 1a) and *Balantidium coli* (fig. 2a) to penetrate the intestinal wall, whereas *Endamoeba coli* (fig. 2a) and *Endolimax nana* (fig. 3a), which are also inhabitants of the intestine do not? It may safely be said, that we really know almost nothing about the mechanism of localization of any human protozoan.

c. *Secondary sites of infection.* Many protozoa become localized in a particular organ or tissue and do not spread to other parts of the body. A few, however, bring about secondary foci of infection in other regions. This requires in the first place either movement on the part of the parasite from one place to another or activities within the host that passively transport the parasite to new situations. The circulatory system of the host is the

most important distributing agency. For example, the dysentery amoeba, *Endamoeba histolytica* (fig. 1a), sets up a primary infection in the large intestine; specimens may enter the blood stream in the capillaries of the intestinal wall and are carried to all parts of the body; frequently the liver becomes a secondary site of infection and an amoebic liver abscess results; less often amoebic abscesses occur in the lungs and brain, and amoebae have been discovered in many other parts of the body. Recently Kofoed (1923) has described dysentery amoebae from bone and believes that they are responsible for Ely's second type of arthritis; he believes also that these amoebae may be the etiological factor in Hodgkin's disease and in some cases of chronic neurasthenia and subnormal health; the evidence for this is as yet incomplete. It is obvious that amoebic abscesses may occur in any part of the body provided local conditions are favorable. Just what factors favor the localization and multiplication of the amoebae in liver, lungs and brain and prevent infections in other parts of the body are not clear.

The details of the distribution and localization of parasites within the host are still to be determined, but it may be said in general that distribution is due primarily to the physiological activities of the host, and localization to host-parasite interactions, the parasites setting up an infection wherever favorable conditions exist.

3. *Passive (natural) resistance of the host*

The number of species of protozoan parasites that are able to bring about infections in man is no doubt very small compared with the number that gain access to his body. The malarial organisms of birds may be inoculated into the

blood of human beings by culex mosquitoes, and the cysts of intestinal protozoa of domesticated animals may be ingested with contaminated food but no infections result. Two principal factors probably account for the success of certain species and the failure of others; these are (1) inability on the part of the parasite to withstand conditions within the host, and (2) failure on the part of the host to provide suitable stimuli for the excystation of encysted forms.

The obstacles that must be met by the parasite at the beginning of an invasion constitute the passive, or natural, resistance of the host. This type of resistance is in part due to the nature of the host without respect to ancestral relations with the parasite or may in part have been built up during the course of evolution as a protection against infection. The changes in the environment of an intestinal flagellate such as *Trichomonas hominis* (fig. 9) which is carried from the outside into the digestive tract of a new host are very striking; light gives way to total darkness; the temperature is constant (98.6°F.); the medium is dense and viscous; chemical conditions become complicated by digestive juices, products of digestion and biochemical products secreted by the host; food conditions are different; and the products of bacterial decomposition are abundant and varied. Somewhat similar changes are encountered when blood-inhabiting species are inoculated into man by mosquitoes (malarial organisms) or tsetse flies (trypanosomes, fig. 18).

A parasite may successfully withstand all these conditions but still fail to bring about an infection because of the absence of factors necessary, for example, to weaken the wall of a protozoan cyst and allow the organism within to escape. The literature of protozoology contains

many reports of human "intestinal" protozoa on the basis of specimens found in the feces which were not active within the intestine but had passed through in the cyst stage and had emerged only after the feces were passed; these are "coprozoic" protozoa, a considerable number of which have been described.

4. *Passive (natural) resistance of the parasite*

If some parasites were not able to overcome the obstacles presented by the host, animals would be totally free from parasites. Thus far no such animal has been discovered. This passive resistance of the parasite, as in the case of that of the host, may have no relation to ancestral infections or may be due in part to evolutionary processes. Whether the resistant coverings of protozoan cysts serve to enable the parasite to reach a certain location within the host or are more important as a protection against injury during their life outside the host it is not possible to decide with certainty. It is known that such cysts will survive when subjected to strong solutions of various chemicals and might therefore easily withstand the body juices of the host. It is also known, as pointed out above in the case of *Trichomonas hominis*, that active trophozoites may pass unharmed through the digestive tract and set up an infection in the cecum. The value of the cyst wall as a means of resisting conditions within the host is therefore very doubtful.

Every animal is able to exist in an environment in which the various factors cover a considerable range, i.e., the optimum conditions are not necessary, although they may be desirable, for the maintenance of either the individual or the race. Protozoan parasites that are natural to a particular host are accordingly able to withstand considerable changes

in temperature; are not affected by the change from light to darkness or *vice versa*; and do not succumb to complex chemical changes nor to increases in the density of the surrounding medium when taken into that host; but why these same parasites are not able to live in nearly related hosts is a problem of great difficulty. Why, for example, is the organism of human malaria able to live in man and not in other species of mammals? Why are the sexual stages of the malarial organism of man stimulated to continued development in the stomach of certain species of anopheline mosquitoes and not in others? Why are the giardias of man unable to live in the duodenum of rats, and those of rats in the duodenum of man? These questions can only be answered when we know more about the passive resistance of the host to the parasite and that of the parasite to the host.

5. *The parasite's method of attack*

The character of the attack of the parasite on the host is of vital importance not only to the host but also to the parasite. It is obvious that the degree of pathogenicity depends on which organs or tissues are invaded, and on the degree and rapidity of tissue destruction or toxin production, since slight injuries inflicted slowly are usually repaired by the host; whereas serious injuries that are quickly produced lead to symptoms. The association that exists in most cases of parasitism is such that the parasite is able to live and reproduce for many years within the host without apparent injury to it. If the host develops severe symptoms both it and the parasites are in danger and if the host dies the parasites die with it. This type of parasitic attack is unusual and is considered to represent a comparatively recent association, since most para-

sites live in harmony with their hosts—a condition that is supposed to have developed during the course of evolution.

Types of parasitism are distinguished largely on the basis of the method of attack of the parasite. Among the amoebae living in man, for example, is *Endamoeba coli* (fig. 2a) which inhabits the lumen of the large intestine where it probably lives on food taken in by the host; this type of parasite is known as a commensal and is sometimes termed a food-robber. It does not live in any other species of host nor outside of the body and is therefore a permanent, obligatory parasite and non-pathogenic. Another species of the same genus, *Endamoeba histolytica* (fig. 1a), also lives in the large intestine of man but feeds on tissue elements which it apparently dissolves with the aid of proteolytic enzymes that it secretes, or engulfs *en masse*. Usually the host is able to repair the tissue as rapidly as it is injured, but often the parasites gain the upper hand and amoebic dysentery results, sometimes ending fatally. This organism is a permanent, obligatory parasite that is always pathogenic and sometimes lethal. Other parasites penetrate tissue cells and develop within them at the expense of the surrounding protoplasm. To this type belong the coccidia that live on cells of the intestinal epithelium and the malarial organisms that destroy red blood cells.

During the destruction of tissues by the malarial parasite there are liberated into the blood debris from the broken-down cells and waste products excreted by the parasite or resulting from digestion within the cell. Besides this, parasitic protozoa may produce toxic substances or zootoxins. Almost nothing is known about these but that they exist is certain and that they act much like bacterial toxins is probable.

6. Changes in the host caused by the parasite

The reactions of hosts to infection may be considered under the headings symptomatology, pathogenesis and immunology. If the parasite lives on the tissues of the body or injures the body in any way it is pathogenic. If the injuries are severe, changes occur in the functions of certain organs sufficient to bring about symptoms. In certain cases the body reacts to the infection by building up a resistance to the parasite which we call immunity.

a. Symptomatology. The symptoms that are characteristic of the various diseases due to parasitic protozoa are in most cases well known. Comparatively little is known, however, regarding the genesis of these symptoms. The Century Dictionary defines a symptom as "one of the departures from normal function or form which a disease presents, especially one of the more evident of such departures." In other words, symptoms arise when the function of an organ is modified. Usually one species of parasitic protozoan brings about a large number of symptoms since more than one organ may be disturbed. Some of these are localized at the point where injury is being done, whereas others appear at a distance.

The most recent and probably the most successful attempt to determine the mechanism of symptom production is that of Sir James MacKenzie (1923). His argument is as follows: Symptoms are produced by organs whose functions are stimulated to unusual activity, or depressed or suspended. Functional activity is dependent on the cells of the organ and on the nerves and other agents that regulate the activity of these cells. There is formed a reflex arc consisting of a receptor which receives the stimulus, an afferent nerve which carries it to a

nerve center, and an efferent nerve which conveys it to the effector. A modification of any part of this arc results in an abnormal response, i.e., a symptom. The effector may be a muscle, gland, or the sensorium.

The genesis of symptoms is open to experimental study, such as that of Brown (1912) on malarial pigment (hematin) as a factor in the production of the malarial paroxysm. Brown obtained hematin from the blood of a rabbit, ox, and dog and used rabbits as experimental animals. Single or divided doses in alkaline solution of from 1.3 to 2.8 mgm. per kilo of body weight were injected intravenously, corresponding to the quantity liberated in cases of human malaria when from 0.3 to 7.5 per cent of the red blood cells are infected. Every dose gave positive results that must have been due to the hematin. There was a definite temperature response in proportion to the dose with a sharp rise to fastigium in about one and one-fourth hours, then a slight fall for from 30 minutes to one hour, followed sometimes by a second rise, and finally a very gradual descent to normal in several hours. Soon after injection the rabbits exhibited convulsive tremors or shivering and the ears became cold—as much as 30°F. below the rectal temperature; this period of chill lasted from 45 minutes to one hour. The paroxysms observed were practically identical with those of human malaria and the conclusion was reached that the toxic action of the hematin is, at least in part, directly responsible for these symptoms.

b. Pathogenesis. Many of the protozoa of man are not pathogenic so far as is known; this is true of *Endamoeba coli* and other commensals. A few, such as *Endamoeba histolytica*, the coccidia and malarial organisms, are unable to exist without direct attacks on the host tissues. These

attacks bring forth more or less definite responses on the part of the host and usually a rather definite series of changes occur during the course of the infection. This series never proceeds beyond the earlier stages in contact carriers (see below) and stops short of the end when the patient is treated or undergoes spontaneous recovery. Only when the death of the host ensues may the final stages be observed. Each parasite maintains its own method of attack and the host responds usually in a perfectly definite way to the inroads of each species of parasite. The changes in the host have definite effects upon the progress of the parasitic attack and it is thus possible to obtain a dynamic view of host-parasite reactions during the course of the infection. The complete pathogenesis has not been worked out for any human protozoon. Experimental studies are possible with lower animals, e.g., amoebiasis in cats, malaria in canaries, trypanosomiasis in rats, etc., and most of what we know of the pathogenesis of protozoan diseases has been gained in this way, but the complete story for any one of them is not yet possible because of lack of observations.

The pathogenesis of intestinal amoebiasis is perhaps as easily studied as that due to any human protozoon. The amoebae are supposed to emerge from the ingested cysts in the small or large intestine. They creep about on the intestinal epithelium and erode the cells by means of a ferment which they apparently secrete. As a result of this the surrounding capillaries become dilated. Continued erosion leads to the formation of ulcers and if the injured tissues are not regenerated rapidly the irritation of the intestinal wall brings on the exudation into the lumen of the intestine of large quantities of serous fluid and peristalsis is greatly increased. The result is diar-

rhea. The formation of purulent and bloody discharges, which are characteristic of dysentery, may follow.

c. Immunology. The subject of immunity to protozoan infections is in its infancy and the little we know about it at present is based on epidemiological observations and on animal experiments. That hosts differ considerably with respect to natural resistance to various protozoan diseases is evident since many individuals do not become infected although they are undoubtedly invaded by the parasites. Acquired resistance has been demonstrated in certain cases. For example, one attack of oriental sore due to *Leishmania tropica* (fig. 22) confers immunity to further infection, and experiments indicate that partial immunity is induced to this organism in dogs and monkeys. On the other hand kala-azar, which is caused by a closely related organism, *Leishmania donovani* (fig. 21), does not produce immunity against reinfection. A tolerance to malaria has been observed and an immunity to this disease may even be acquired. Thus children in an endemic region become infected when infants and, if they recover, may be reinfected year after year until by the time they are ten years old they cease to show symptoms although they possess enlarged spleens and have parasites in their blood. When these children become adults they are immune as evidenced by a decrease in the size of the spleen and by the absence of parasites from the blood.

Very little is known about the resistance of man to trypanosome infections but a number of important investigations have been carried on with animals. The most important recent researches are those of Taliaferro (1926) with *Trypanosoma lewisi* in rats. If no resistance were encountered when trypanosomes are inoculated into an experimental animal the

organisms would increase according to a geometrical progression series and the death of the host finally ensue. This is what appears actually to occur when *Trypanosoma brucei* is inoculated into a rat. If the parasites do not increase in this way then some type of resistance is in operation. In infections of rats with *T. lewisi* three types of resistance become manifest "(1) the retardation and final inhibition of reproduction by about the tenth day, (2) the sudden destruction of the majority of the parasites between the eighth and twelfth days, and (3) the eventual total destruction of the parasites which terminates the infection and may take place from a few days to several months after the first crisis." Taliaferro has demonstrated the formation of a reaction product in the blood serum which totally inhibits the reproduction of the trypanosomes by about the tenth day. Serum from such an animal when injected into a fresh rat will prevent the reproduction of trypanosomes in it thus furnishing an excellent example of the passive transfer of the immunity from an infected to an uninfected animal. There is no definite evidence as to what causes the destruction of most of the trypanosomes between the eighth and twelfth days but the blood serum evidently acquires rather suddenly a trypanolytic property. The final destruction of trypanosomes which terminates the infection seems to be due to a lysin. The immunology of protozoan infections presents a large and fascinating field for investigation.

7. Changes in the parasite due to residence in the host

a. Immunology. Residence in a host may bring about the building up of an active, acquired resistance on the part of the parasite in certain cases. The

well-known hypothesis of Welch (1902), that bacteria are stimulated to protect themselves by the production of antibodies when they are subjected to the defensive forces of the host, no doubt holds true for protozoa. That this should occur is not at all strange since parasites are living organisms and doubtless react to various stimuli much as does the host. Not only are parasites supposed to actively protect themselves from the host, but they appear to be capable of modifications that enable them to resist harmful therapeutic agents. Thus races of parasites are supposed to develop that are "fast" to substances ordinarily destructive. For example, it is customary to speak of arsenic fastness in trypanosomes and quinine fastness in malarial organisms. If trypanosomes are subjected to a dose of an arsenical insufficient to destroy them, they become more resistant to arsenic than they were at the beginning. Repeated doses increase the resistance. That this result is not due simply to the selecting out of more resistant natural strains is indicated by the fact that Oehler (1913) obtained a resistant strain in a pure line infection. The resistance may persist for a long time, e.g., after passage through 400 animals, during which many thousands of asexual generations must have occurred. Loss of this resistance may follow passage through a different species of laboratory animal or through the invertebrate host.

b. Aggressivity. The term aggressivity is applied to the invasive powers of a parasite. Changes in parasite aggressivity seem to occur due to residence within a host and may be illustrated by several examples. Epidemics of malaria have been described occurring in endemic regions. No one has satisfactorily explained this phenomenon. Parasites that were extra-virulent may have been

brought in from some other region, or the resistance of the general population may have decreased all at once thus enabling the organisms already present to undergo rapid increase in numbers, but it is possible that these epidemics are due to an increase in the invasive powers of the organisms responsible for the endemic malaria of the region.

Differences in invasive powers have been noted among the cysts of the dysentery amoeba, *Endamoeba histolytica*, which may have been due to changes during residence in the human host. For example, Baetjer and Sellards (1914) state that "chronic cases of long standing, with mild symptoms, often produced an attack in animals which was of comparatively short duration and eventually ended in recovery;" and Wagener and Thomson (1924) were able to infect kittens without difficulty with amoebae from an acute case of amoebiasis, but succeeded in only one of fourteen kittens when amoebae were used from a chronic case of amoebiasis. The supposition is that the conditions of chronicity modified the aggressivity of the amoebae until a strain with very little invasive powers was developed.

8. Host parasite adjustments during an infection

a. Carriers. During the course of a natural infection as outlined above various adjustments occur between host and parasite. Continued reproduction by the parasite without check would obviously result in the death of the host; this would be a disadvantage to the parasite, since it is thus prevented from further growth and multiplication and especially from dissemination. Spontaneous recovery results in most cases of protozoan infection, but by recovery is meant the cessation of symptoms and not the total disappearance of

parasites from the body. Frequently the host by means of its acquired resistance is able to destroy most but not all of the parasites, and hence to bring about the carrier condition.

A carrier is a host in which parasites live and by which they are disseminated but exhibits no visible symptoms of infection. Walker and Sellards (1913) distinguished two types of carriers in their work with human amoebae, (1) contact carriers who are parasitized but never have exhibited symptoms, and (2) convalescent carriers who have recovered from the disease but are still infected. This is the ideal condition for the parasite since it is not in danger of losing its host and is ensured of the distribution of its offspring. As a matter of fact most host-parasite relationships are of this type; hosts become infected but never show symptoms and are apparently none the worse because of the presence of the parasite, a sort of equilibrium between host and parasite being established. Certain species of hosts are almost universally infected by certain species of parasites in nature and the parasitized condition might almost be considered the normal state for these species.

Infection without symptoms is supposed to be the result of long periods of association. According to this view the length of parasitism of a certain species of host by a certain species of parasite can be determined approximately by the host-parasite reactions. For example, if a parasite is pathogenic and lethal for a certain host the association is supposed to be recently acquired whereas the absence of symptoms indicates a long period of consociation. Frequently carriers are spoken of as reservoirs since they are store houses for the organisms that are responsible for the spread of the parasite to new hosts. In certain cases the para-

site is infective both to man and to lower animals and one or both kinds of hosts may serve as reservoirs. Very little is known at present regarding the conditions underlying the carrier state.

b. Latency. Similar in certain respects to the carrier condition is the state known as latency. When parasites are present in a host but do not make themselves manifest, they are said to be latent. Latency, however, does not necessarily require the dissemination of the parasites by the host. In some cases a host may be parasitized and show no symptoms; in other cases a host may recover from symptoms but still harbor parasites; both types of conditions may be included under the term latency. Certain changes in host or parasite may bring on symptoms in a host that had never previously exhibited evidences of infection; such a case might be considered one with an extended incubation period.

c. Relapse. Symptoms may appear in a host that had previously shown symptoms but had apparently recovered; such a reappearance of symptoms is known as a relapse if the latent period is short and a recurrence if the latent period is long. Relapses may be induced in certain infections by definite stimuli but the physiological bases for this have not been determined.

Perhaps the host-parasite relationship resulting in the carrier condition, latency and relapse may best be illustrated by facts derived from the study of malaria in man and birds. Relapse is in certain respects the most important phase of malaria, since it is largely responsible for the maintenance of the race from year to year. For example, the malarial organism does not pass the winter in the mosquito in our Southern States but lives during this period only in man. In the spring human carriers have relapses, numerous gameto-

cytes (fig. 26c, 27c, 28c) appear in their blood and from them the mosquitoes become infected. If relapse could be prevented the mosquitoes would have no chance of becoming infected and malaria would soon die out.

Many cases have been described of primary latency in malaria, i.e., the appearance of symptoms months or years after infection, although the normal incubation period is three weeks or less. In these cases parasites had no doubt been present in small numbers but unable, because of some sort of host resistance, to increase sufficiently to cause symptoms until a change took place in the physiological state of the host which broke down this resistance. During the normal course of a malarial infection the parasite number rises to the peak then falls, and finally becomes so small that no parasites are to be found in the blood when examined by routine methods. Symptoms cease as the parasite number falls. Frequently parasites appear again in large numbers and symptoms are again experienced after an interval of a few days or weeks, showing that not all of the parasites were destroyed at the end of the primary attack.

Various theories have been advanced to account for such cases of relapse. The theory with most evidence in its favor is that proposed by Ross. According to this a few parasites remain in the host after symptoms cease, and these are able to maintain the race by asexual reproduction. Work done in this laboratory with bird malaria seems to prove the correctness of this theory. Dr. Ben-Harel (1923) showed that during the period between the cessation of symptoms and the appearance of a relapse, malarial organisms are present in the internal organs undergoing asexual reproduction. Dr. Lucy G. Taliaferro (1925) further proved

that asexual reproduction during this period continues at the same rate as during the period of symptoms. The conclusion is that the rate of reproduction is not changed, but most of the offspring must be destroyed in some way at present unknown. If the physiological state of the body is changed these parasites are not destroyed as fast as they are produced and a relapse ensues. The subcutaneous or intra-muscular injection of various substances called provocatives is capable of bringing about this result. Some of these are adrenalin, ergotin, salvarsan, and strychnin. Relapse may also be brought about by radiation with ultraviolet light (Whitmore, 1923) and frequently results from exposure to cold or sun, from inebriation, errors in diet, surgical operations, etc. It seems probable that these various stimuli cause some change in the blood favorable to the parasite, such as an increase in sugar content; experiments are now in progress to test this hypothesis.

9 Therapeutics

Host-parasite relationships may be profoundly modified by treating the host. This may take the form of building up the resistance of the host (biological therapy) or of destroying the parasite either directly or through the host (chemical therapy).

a. Biological therapy. Constitutional biological therapy involves the usual procedures for maintaining or increasing natural host resistance, such as rest, minimum movement, and the treatment of other infections when present. Often the host may be aided by a certain type of nourishment. For example, a milk diet is prescribed in cases of intestinal amoebiasis since milk produces a small amount of putrefaction and is practically all absorbed before it reaches the large

intestine where the amoebic ulcers are located.

Vaccines, antitoxins, etc., that increase the active resistance of the host are not available for protozoan diseases. There seem, however, to be no insurmountable obstacles to their preparation and use. A close approach to vaccination is the custom reported to have been prevalent among the Jews of Bagdad who infected their children with the organism of oriental sore (*Leishmania tropica*, fig. 22) by direct inoculation since they had learned that one attack gave immunity to further attacks; it was thus possible to infect unexposed parts of the body and avoid sores that might otherwise appear on the face.

An interesting zootoxin was obtained by Pfeiffer (1891) from *Sarcocystis tenella*, a sporozoan muscle parasite of sheep which Laveran and Mesnil (1909) named sarcocystin. This substance is highly toxic and 0.0001 gram per kilo of body weight is fatal to rabbits. Teichmann and Braun (1911) by immunizing rabbits obtained an effective antitoxin and McGowan (1913) found that the serum of infected sheep gave positive complement fixation.

b. Chemotherapy. Drugs may be used to aid the host either as parasitocides by destroying the parasites or as agents for building up host resistance. In many cases it is difficult to determine which of these processes is taking place. There seems to be no reason why, in the case of intestinal infections, enemas containing drugs toxic to protozoa should not be effective parasitocides. Thus rectal irrigations with a solution of tannic acid or of bihydrochloride of quinine have been recommended in cases of amoebic dysentery, and rectal injections of iodine solution or of methylene blue for flagellate infections. Such treatment might be ef-

ficacious against organisms such as the flagellate *Trichomonas hominis* which lives in the lumen of the large intestine but probably does not destroy organisms such as endamoebae and coccidia that live in the wall of the intestine. In a similar fashion certain investigators advise vaginal douches with a saturated solution of sodium bicarbonate to destroy the flagellate *Trichomonas vaginalis* (fig. 7), which ordinarily lives in the acid secretions of the vagina.

It seems possible that drugs taken by mouth may act directly upon the parasites within the intestine. *Iodamoeba williamsi* (fig. 4a) is destroyed by the administration of emetine although it lives in the lumen of the intestine. In this case the emetine may kill the parasite by actual contact. Drugs injected into the blood stream may likewise destroy blood inhabiting protozoa.

Progress in the chemotherapy of protozoan infections has been most gratifying within the past two decades. Quinine was already in use in the seventeenth century as a cure for malaria but only recently have satisfactory therapeutic agents for other protozoan diseases been discovered. Emetine was introduced by Sir Leonard Rogers for amoebic dysentery in 1912 and soon came into general use; more recently yatren and stovarsol have both been proven to be specific agents for the cure of this disease. In 1905 Thomas inaugurated the treatment of trypanosomiasis with atoxyl and to this have since been added tartar emetic, tryparsamide, Bayer 205 and Pasteur 309. Tartar emetic which was also found by Vianna (1913) to be efficacious against American leishmaniasis, has been found to be equally valuable for the treatment of kala-azar and oriental sore. No therapeutic agents are yet available for intestinal flagellates and coccidia.

Whether these drugs act directly on the parasite or through the host is still in doubt. In a recent illuminating address Dale (1925) states the situation in the following words. "The conception of a remedy not killing the parasites immediately, but modifying their virulence, or lowering their resistance to the body's natural defences; of a remedy not acting as such, but in virtue of the formation from it in the body of some directly toxic product, either by a modification of its structure or by its union with some tissue constituent; of an affinity of the remedy for certain cells of the host's body, leading to the formation of a depot from which, in long persistent, never dangerous concentration, the curative substance is slowly released; all these conceptions present themselves, again and again, as necessary for our present rationalisation of the effects observed. It can hardly be doubted that they will potently influence the methods by which, in the immediate future, new and still better specific remedies are sought. But though our practical aim, in relation to the affinities of a remedy for the parasite and for the host's tissues, may be radically changed the meaning of these specific affinities, so delicately adjusted to a precise molecular pattern, remains dark."

10. Route taken by parasites in escaping from the host

As already noted, parasites must not only reproduce within the host but their offspring must be able to escape and set up new infections in order to maintain the race. In most cases escape is easy since the parasites attack parts of the host from which natural channels lead to the outside; e.g., intestinal protozoa pass out with the feces. The escape of sufficient trichomonads from the mouth

and vagina to keep these races from dying out is probably brought about by kissing and coitus respectively. The blood-inhabiting protozoa depend upon intermediate bloodsucking hosts for their liberation and dissemination and a truly wonderful series of developmental stages on the part of the parasite and reactions on the part of the host and intermediate host are necessary to accomplish this. The life-cycles of some parasites are so complicated that their survival seems almost impossible.

Other methods of escape are exhibited by protozoan parasites of certain lower animals. Some parasites are set free by the death and decay of the host; others live in an intermediate host that is captured and devoured by the definitive host; some are liberated in the digestive tract of an animal that eats the host, and pass out in its feces; a few species form tumors which break open and allow the parasites to reach the outside; and in some cases the parasites pass from one host to another in the eggs of the intermediate host ("hereditary" transmission).

V. HOST-PARASITE SPECIFICITY

By host-parasite specificity is meant the character of the relationships between species of parasites and species of hosts with respect to host susceptibility and parasite infectivity. Hosts and parasites may be divided into groups and labelled according to their interspecific relations, since observations and experiments have built up a considerable body of facts regarding this subject; but what environmental conditions and host and parasite characteristics are responsible for the facts observed are still very obscure.

1. Host susceptibility

Parasitologists have long recognized different types of hosts with respect to

their susceptibility to various parasites. Thus if a host is easily parasitized by a certain species it is said to be tolerant, whereas if it is difficult to parasitize it is classed as refractory. A host that is frequently found parasitized by a certain species in nature is known as a natural or autochthonous host; whereas one that does not become so parasitized may be considered a foreign host. If a species of parasite that habitually lives in a certain host species is found in a host that is very seldom infected, that host is spoken of as an accidental or casual host. A host may become infected but throw off the infection after a short time, in which case it is known as a provisional or transitory host; or it may serve as a host for a short stage in the life-cycle of a parasite, thus becoming a temporary host.

Frequently it is possible to infect species of hosts in the laboratory that do not become infected, as a rule, in nature, either because their habits are such that they do not come into proper relations with the parasites or because they are refractory except when large numbers of parasites are present or when these are administered to them in certain definite ways not usually possible in nature. Thus cats are relatively easily infected by laboratory procedure with *Endamoeba histolytica*, the dysentery amoeba of man, but are almost never found to be infected in nature.

Whether or not a susceptible species of animal becomes infected with a particular species of parasite in nature depends primarily on three factors; (1) animal and parasite must live in the same geographical region, (2) the habits of the animal must be such as to bring it into proper relations with the infective stage of the parasite, and (3) the life-cycle of the parasite must be such that its infective

stage is reached when and where the host is available to be parasitized.

The first factor mentioned is so obvious that little discussion is necessary. The absence of certain diseases from certain regions is frequently due not to the absence of susceptible hosts but to the absence of the parasites. This, for example, may account for the absence of malaria from countries where susceptible human hosts and the proper species of anopheline mosquitoes exist but where the malarial parasites have never been introduced. On the other hand, many cases might be cited of diseases that have appeared in various regions previously free from them because of the introduction of the causative parasite.

The other two factors are really the same considered from the two standpoints of host and parasite respectively. If the life-cycle of a parasite and the activities of its natural host are studied side by side it will appear as though both host and parasite were actually trying to bring about a situation favorable for infection. For example, the gametocytes of the malarial organisms (fig. 26c, 27c, 28c) live in the peripheral blood where they cannot fail to reach the stomach of the mosquito that sucks up the blood; the infective sporozoites congregate in the salivary glands of the mosquito where they seem to lie in wait to be inoculated into a new host. The mosquito lives on the blood of man and thus enables the parasites to enter the blood stream; whereas it might live on fruit juices as it is able to do in the laboratory. The infective mosquito bites usually at night when the host is asleep and is thus able to inoculate the sporozoites successfully during an uninterrupted meal. A change in any one of these conditions might easily bring about the annihilation of the race of parasites;

for example, if the gametocytes were localized in the internal organs of man or if the sporozoites did not reach the salivary glands of the mosquito there would be no spread of malaria and the disease would soon die out.

An infection may be acute, malignant, fulminating, chronic or benign, but the evidence does not indicate that the susceptibility of the host to an infection has any bearing on the character of the infection induced. That is to say, a host may be more susceptible to infection, and probably usually is, by a species of parasite that never calls forth symptoms than by a pathogenic or lethal species.

2. *Parasite infectivity*

If a host is easily parasitized by a species, the parasite is said to be highly infective. How much its infectivity is due to the host and how much to the parasite it is impossible to say. Several of the terms noted above with respect to hosts are also commonly used to designate different types of parasites. Thus, we speak of natural parasites, accidental parasites, and provisional, transitory or temporary parasites. Parasites are also classified according to the necessity of existence within a certain host as facultative, when this is not required, and obligate, when the parasite is unable to live in any other host. The invasive powers of a parasite are indicated by such terms as virulent or aggressive and the degree of infectivity with respect to the effects on the host as pathogenic, sublethal, and lethal.

The data regarding some phases of host-parasite relationships in malaria and intestinal protozoa will serve to indicate some of the problems involved in parasite infectivity. (1) The malarial organisms of man can complete their sexual cycle only in the mosquito. Gametocytes of

both sexes may be present in the blood but do not undergo maturation and fertilization as long as they remain there. If an anopheline mosquito of a certain species sucks malarious blood into its stomach the "ripe" gametocytes are stimulated into activity, whereas all the parasites in other stages of the asexual or sexual cycle are destroyed. Maturation, fertilization, the formation of oökinetes, oöcysts, sporoblasts and sporozoites all proceed in regular order and finally fully developed sporozoites congregate in the salivary glands and the mosquito is ready to pass on the infection to a susceptible human host. Not all anopheline mosquitoes are equally capable of infection; many of them are quite refractory and some that appear never to be infected in nature may be parasitized in the laboratory. If mosquitoes of other types, e.g., the common culicines, ingest malarious blood the "ripe" gametocytes as well as all other stages of the parasite are destroyed. The problem here is why are these parasites infective to one species of mosquito and not to a nearly allied species living in the same region and therefore subjected to the same external conditions, and feeding on the same organic material, namely the blood of man or of lower animals. Differences in infectivity are probably due to failure on the part of the gametocytes to resist some agent or agents in the stomach of the refractory host or to the absence *in toto* or in part in that type of host of the agents that stimulate further development.

(2) The intestinal protozoa of man that are transmitted in the cyst or oöcyst stage offer a similar problem. Why do some cysts pass through the entire intestine without apparent change; whereas the cyst walls of others break down and the organisms within are stimulated to develop? Is the difference due to dif-

ferences in the composition or thickness of the cyst walls or failure of the environment to stimulate activity within the cyst which results in the dissolution of the cyst wall from within? It is evident that factors exist either in the parasite or in the host or in both that account for host susceptibility and parasite infectivity and bring about the conditions that exist in nature, where most parasites seem to be limited to one or a very few species of hosts, being unable to infect other species, usually even those closely allied.

The two extremes of host-parasite specificity may be illustrated by the relations we have found in this laboratory to exist between (1) the giardias of mammals and (2) the herpetomonad flagellates of flies. Within the past few years we have been carrying on a series of investigations (Simon, 1921, 1922; Hegner, 1922, 1923, 1924, 1925) which seem to indicate that the giardias found in each species of host differ specifically from those found in every other species of host and only in a few cases is more than one species of host infected by one species of giardia. Thus morphologically distinct species have been described from tadpoles, house mice and rats, field mice, rabbits, cats, dogs, guinea pigs, and ground squirrels as well as from certain birds and reptiles. Here then is an example of very rigid host-parasite specificity.

In contrast to this are the results of Becker's (1923) studies on the herpetomonad flagellates that live in the intestine of flies. Investigators previous to Becker's work assumed that each species of fly was infected with its own peculiar species of herpetomonad and hence when a new species of fly was found to be infected the organism was given a new specific name. Becker carried on experiments with six species of muscoid flies

belonging to six different genera and found that each species could be infected with herpetomonads from each of the other five species. Because of these results and of the fact that no morphological differences could be observed between the various so-called species, Becker concludes that the flagellates from these six species of flies are all of the same species,—that first described from the house fly, *Musca domestica*, as *Herpetomonas muscae-domesticae*. These results have been confirmed and extended by Drbohlav (1925).

To account for different degrees of host susceptibility and parasite infectivity we must refer again to certain phases of host-parasite relationships already discussed and call attention to several factors not yet mentioned. The most important of these are the natural resistance of the host and parasite, acquired susceptibility of the host, acquired infectivity of the parasite, and changes in the environment within the host. Because of both lack of space and lack of knowledge, only some of the problems will be mentioned here and no attempt will be made to account for the conditions described.

That hosts differ in susceptibility to a given parasite has been abundantly demonstrated. The difference may be racial, familial, or individual, i.e., it may be inherited. It would be interesting to study this subject with hybrids between susceptible and nonsusceptible hosts. Sex and age may also have a profound effect on host-parasite specificity. In general young animals are more susceptible to infection than adults. This was found to be true, for example, by Maxcy (1921) for *Giardia lamblia* in children examined at the Johns Hopkins Hospital.

The physiological state of the host may have an important bearing on its

susceptibility. Frequently a refractory host may become infected if his resistance is lowered by overwork, by previous infection with other parasites, by malnutrition, by intoxication, by exposure to wet and cold, by trauma, or by shock. Changes in physiological state no doubt also take place in parasites which raise or lower their powers of infectivity. Other factors that cause no inconvenience to the host may be unfavorable for the parasite. For example, the writer (Hegner 1924, 1925) has called attention to the fact that intestinal protozoa are rarely present in carnivorous animals. He had previously (Hegner, 1923) shown that rats fed throughout their lives on a largely carnivorous diet that was favorable for growth and reproduction were free from intestinal protozoa and that rats heavily infected with intestinal flagellates can be largely freed from their infection, especially with trichomonads, if fed for about a week on such a diet. Presumably rats that are being fed on this diet would not become infected if the parasites were introduced with their food. The change from a largely vegetarian diet to one largely carnivorous brings about great modifications in the bacterial content of the cecum, modifications that the trichomonads are apparently unable to resist.

Opportunities for the study of the effects of the environment upon host susceptibility and parasite infectivity are presented among lower animals with respect to such factors as temperature, diet, starvation, and gas content of the air. Cleveland (1924, 1925, 1926) has carefully studied these factors in the case of termites and their intestinal flagellates. He finds that the four principal species of flagellates of these insects are affected differently by changes in temperature, by starvation and by subjection to oxygen

under pressure. He was able to prove that the termites are unable to live without intestinal flagellates to digest cellulose for them, and that the flagellate *Streblomastix* is not a symbiote but probably receives its nourishment from the other protozoa.

The origin of host-parasite specificity is really synonymous with the evolution of parasitism. It is obvious, as already pointed out, that parasitism cannot exist unless the hosts and parasites involved are present in the same region and behave in such a way as to come frequently into contact. If these conditions are fulfilled, the factors that make it possible for the parasite to live and reproduce within the host present themselves for consideration. Thus it seems certain that man often takes in with his food the infective stages of many parasites of lower animals, e.g., the cysts of giardias of rats and mice, and the oöcysts of coccidia of cats, dogs and rabbits; and that his blood stream is inoculated frequently by culicine mosquitoes with the organisms of bird malaria. These organisms are not able to remain in the body of man because man does not tolerate them.

But what factors are responsible for tolerance or refractoriness and how have these conditions arisen in the course of evolution? Some of the factors involved have been discussed above and, as we have seen, are still very obscure. Our account has been based on the conditions of host and parasite as we find them today without much consideration of how the present status has been reached. There can be little doubt, however, but that long association has brought about changes in both host and parasite which make it possible for them to live together in harmony except under special conditions. An increase in the virulence

of the parasites might disturb the equilibrium established and bring about pathological conditions in the host; a decrease in the resistance of the host might have the same effect; or a decrease in the aggressivity of the parasite might prevent infection; and an increase in the resistance of the host might also prevent infection.

VI. CONCLUSION

In conclusion a few remarks may not be out of place regarding the scientific and practical importance of investigations of host-parasite relationships. Biologists interested in this field are searching for the truth without special attention to its effect upon human welfare. They will be satisfied only when all the various phases of the subject have been made clear. New data reveal new problems and the program is thus undergoing constant modification. There is no fear of exhausting the subject, since each step in advance brings us closer to the fundamental problems of life and discloses new and ever more fascinating questions to be solved.

No special section of our program is devoted to the practical aspects of host-parasite relationships. These, however, are always kept in mind and any new data obtained are always scrutinized for possible applications to prevention and control. Our investigations are of importance from the standpoint of personal hygiene since they furnish the knowledge necessary to protect the individual from protozoan infections. Of even greater significance are the data of use to workers in the field of public health since whole communities may be protected as a result of these scientific investigations.

Finally there is always before us the possibility of throwing light on the greatest of all of our problems, that of

the origin and evolution of parasitism. The materials available for observation and experiment are particularly favorable for attacks on this problem, and as an added incentive is the knowledge that

the elucidation of the changes that occur during the development of the parasitic from the free-living habit may furnish the key to the solution of the problem of the method of evolution.

LIST OF LITERATURE

- BAETJER, W. A., and SELLARDS, A. W. 1914. The behavior of amoebic dysentery in lower animals, etc. *Bull. Johns Hopkins Hosp.*, 25: 237-241.
- BECKER, E. R. 1923. Transmission experiments on the specificity of *Herpetomonas muscae-domesticae* in muscoid flies. *Journ. Parasit.*, 10: 25-34.
- BLACKLOCK, B., and YORKE, W. 1922. The Trypanosomiasis. In Byam and Archibald; the Practice of Medicine in the Tropics. 2: 1386-1443.
- BOYD, G. H. 1925. The influence of certain experimental factors upon the course of infections with *Plasmodium praecox*. *Amer. Journ. Hyg.*, 5: 818-838.
- BROWN, W. H. 1912. Malarial pigment (hematin) as a factor in the production of the malarial paroxysm. *Journ. Exp. Med.*, 15: 579-597.
- CAULLERY, M. 1922. Parasitism and symbiosis in their relation to the problem of evolution. Smithsonian report for 1920: 399-470.
- CAULLERY, M. 1922. La Parasitisme et la Symbiose. 400 pp. Paris.
- CHANDLER, A. C. 1923. Speciation and host relationships of parasites. *Parasit.*, 15: 326-339.
- CHRISTOPHERS, S. R. 1922. Malaria: endemology and epidemiology. Byam and Archibald's Practice of Medicine in the Tropics. 2: 1546-1554.
- CLEVELAND, L. R. 1923. Correlation between the food and morphology of termites and the presence of intestinal protozoa. *Amer. Journ. Hyg.*, 3: 444-461.
- CLEVELAND, L. R. 1924. The physiological and symbiotic relationships between the intestinal protozoa of termites and their host, with special reference to *Reticulitermes flavipes* Kollar. *Biol. Bull.*, 46: 177-225.
- CLEVELAND, L. R. 1925. The effects of oxygenation and starvation on the symbiosis between the termite, *Termopsis*, and its intestinal flagellates. *Biol. Bull.* 48: 309-326.
- CLEVELAND, L. R. 1926. Symbiosis among animals with special reference to termites and their intestinal flagellates. *Quart. Rev. Biol.* 1: 51-60.
- COVENTRY, F. A. 1925. The reaction product which inhibits reproduction of the trypanosomes in infections with *Trypanosoma lewisi*, with special reference to its changes in titer throughout the course of the infection. *Amer. Journ. Hyg.*, 5: 127-144.
- DALE, H. H. 1924. Progress and prospects in chemotherapy. *Science*, 60: 185-191.
- DOBELL, C. 1919. The Amoebae Living in Man: A Zoological Monograph. London, 155 pp.
- DOBELL, C., and O'CONNOR, F. W. 1921. The Intestinal Protozoa of Man. 211 pp. London.
- DRBOHLAV, J. J. 1925. Studies on the relation of insect flagellates to leishmaniasis. *Amer. Journ. Hyg.*, 5: 580-621.
- HEGNER, R. W. 1922a. The systematic relationship of *Giardia lamblia* Stiles, 1915, from man and *Giardia agilis* Kunstler, 1882, from the tadpole. *Amer. Journ. Hyg.*, 2: 435-441.
- HEGNER, R. W. 1922b. A comparative study of the giardias living in man, rabbit, and dog. *Amer. Journ. Hyg.*, 2: 442-454.
- HEGNER, R. W. 1923. The effects of changes in diet on the incidence, distribution and numbers of certain intestinal protozoa of rats. *Amer. Journ. Hyg.*, 3: 180-200.
- HEGNER, R. W., and TALIAFERRO, W. H., 1924. Human Protozoology. 597 pp. New York.
- HEGNER, R. W. 1924. The relations between a carnivorous diet and mammalian infections with intestinal protozoa. *Amer. Journ. Hyg.*, 4: 393-400.
- HEGNER, R. W. 1925. Intestinal flagellates in Tropical America. *Amer. Journ. Trop. Med.*, 5: 239-245.
- HEGNER, R. W., and ANDREWS, J. M. 1925. Effects of a carnivorous diet on the intestinal pH of rats with reference to flagellates. *Amer. Journ. Hyg.*, 5: 557-558.
- HEGNER, R. W. 1925. Medical Research in Malaria. *Southern Med. Journ.*, 18: 438-440.
- HEGNER, R. W. 1925. *Giardia felis* n. sp., from the domestic cat and giardias from birds. *Amer. Journ. Hyg.*, 5: 258-273.

- HEGNER, R. W. 1925. *Trichomonas vaginalis* Donné. Amer. Journ. Hyg., 5: 302-308.
- HEGNER, R. W. 1925. Excystation in *Giardia lamblia* from man. Amer. Journ. Hyg., 5: 250-257.
- HOLMES, F. O. 1925. The relation of *Herpetomonas elmassiani* (Migone) to its plant and insect hosts. Biol. Bull., 49: 323-337.
- JAMES, S. P. 1922. Malaria: pathology, symptomatology, diagnosis, treatment. Byam and Archibald's Practice of Medicine in the Tropics. 2: 1568-1598, 1621-1653.
- JAMES, S. P., and CHRISTOPHERS, S. R. 1922. Malaria. Byam and Archibald's Practice of Medicine in the Tropics. 2: 1500-1515, 1599-1620.
- KENDALL, A. I. 1913. Saprophytism, parasitism and pathogenism. Boston Med. and Surg. Journ., 169: 749-753.
- KOFOID, C. A. 1923. The life cycle of the protozoa. Sci., 57: 397-408.
- KOFOID, C. A. 1923. Amoebae and Man. Univ. Calif. Chron. (1923): 149-310.
- LAVERAN, A., and MESNIL, F. 1909. De la Sarcocystine, toxine des Sarcosporidies. C. R. Soc. Biol. 41: 311.
- LAVERAN, A. 1917. Leishmanioses. Paris. 521 pp.
- LAVERAN, A., and MESNIL, F. 1912. Trypanosomes et trypanosomiasis. Paris. 1000 pp.
- MACKENZIE, SIR JAMES. 1923. The principles of symptomatology: an introduction to a new outlook in medicine. Lancet 205: 963-968, 1020-1024, 1069-1075.
- MAXCY, K. F. 1921. *Giardia (Lamblia) intestinalis*; a common protozoan parasite of children. Johns Hopkins Hosp. Bull. 32: 166-170.
- M'GOWAN, J. P. 1913. The toxic action of sarcosporidial muscles as obtained from "scrapie" sheep. Journ. Path. Bact., 18: 125-126.
- NUTTALL, G. H. F. 1923. Symbiosis in animals and plants. Physiology, 1-17.
- OEHLER, R. 1913. Zur Gewinnung reiner Trypanosomenstämme. Centralb. Bakt. und Parasit. Orig., 70: 110-111.
- OSBORN, H. F. 1921. Parasitism as a factor in disease. Sci., 54: 99-108.
- PEARCE, L. 1925. Trypsamide treatment of African sleeping sickness. Sci., 61: 90-92.
- PFEIFFER, L. 1891. Die Protozoen als Krankheitserreger. 2 Aufl. Jena.
- ROOT, F. M. 1921. Experiments on the carriage of intestinal protozoa of man by flies. Amer. Journ. Hyg., 1: 131-153.
- ROSS, SIR RONALD. 1911. The prevention of malaria. 2 ed. 711 pp. London.
- SIMON, C. E. 1921. *Giardia enterica*; a parasitic intestinal flagellate of man. Amer. Journ. Hyg., 1: 440-491.
- SIMON, C. E. 1922. A critique of the supposed rodent origin of human giardiasis. Amer. Journ. Hyg., 2: 406-434.
- SMITH, T., and KILBORN, F. L. 1893. Investigations into the nature, causation and prevention of southern cattle fever. Report Bur. Animal Industry, U. S. Dept. Agric., (1893): 177-304.
- TALIAFERRO, W. H., and TALIAFERRO, L. G. 1922. The resistance of different hosts to experimental trypanosome infections, with especial reference to a new method of measuring this resistance. Amer. Journ. Hyg., 2: 264-319.
- TALIAFERRO, L. G. 1925. Infection and resistance in bird malaria, with special reference to periodicity and rate of reproduction of the parasite. Amer. Journ. Hyg., 5: 742-789.
- TALIAFERRO, W. H. 1926. Host resistance and types of infection in trypanosomiasis and malaria. Quart. Rev. Biol. 1: 246-269.
- TRICHMANN, E., and BRAUN, H. 1911. Ueber ein Protozoentoxin (Sarkosporidiotoxin). Arch. Protist. 22: 351-365.
- THOMSON, J. D., and WOODCOCK, H. M. 1922. The parasites of malaria. Byam and Archibald's Practice of Medicine in the Tropics, 2: 1516-1546.
- WAGNER, E. H., and THOMSON, M. D. 1924. Experimental amoebiasis in cats from acute and chronic human cases. Univ. Calif. Pub. in Zool., 26: 267-280.
- WALKER, E. L. 1913. Experimental balantidiosis. Phil. Journ. Sc. (B) 8: 333-349.
- WALKER, E. L., and SELLARDS, A. W. 1913. Experimental entamoebic dysentery. Philip. Journ. Sci., (B. Trop. Med.) 8: 253-331.
- WELCH, W. H. 1902. Recent studies of immunity with special reference to their bearing on pathology. Brit. Med. Journ., 2: 1105-1114.
- WENTON, C. M. 1915. The development of the oöcyst of the human coccidium: an addendum. Lancet, 2: 1296.
- WENTON, C. M. 1923. Coccidiosis of cats and dogs and the status of the *Isospora* of man. Ann. Trop. Med. and Parasit., 17: 231-288.
- WENTON, C. M., and O'CONNOR, F. W. Human Intestinal Protozoa in the Near East., 218 pp. London.
- ZIEMANN, H. 1924. Malaria und Schwarzwasserfieber. 592 pp. Leipzig.



THE MATURATION DIVISIONS IN RELATION TO THE SEGREGATION OF HOMOLOGOUS CHROMOSOMES

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I. INTRODUCTION

THE discovery of new facts and their correlations with each other and with those previously known may satisfy the individual research worker, but the practical applications of the facts hold the chief interest for those in other fields of endeavor. Thus, cytology principally interests the public on account of its relation to pathology, to physiology, and to evolution and heredity. Its relationship to the last of these is the especial concern of the present paper.

Living things, plant or animal, are either single cells as in the lower forms of life or coördinated groups of many cells as in all higher organisms. In other words, the unit of living matter is the cell. This is a microscopical bit of protoplasm which contains a highly specialized, centrally-located part called the nucleus. The essential constituent of the nucleus is a substance which stains deeply with basic dyes, hence Flemming ('79) named it chromatin from the Greek word *χρῶμα* meaning color. Concor-
dant evidence from many lines of work has been sufficient to convince most biologists that chromatin, which is the only material contributed in equal amount by both parents in fertilization, is the physical basis of heredity. The chromatin is in a loose, spongy condition during the ordinary processes of metabolism,

but condenses when a cell prepares to divide. It then becomes evident that there is a definite number of dense bodies which were named chromosomes by Waldeyer in 1888. During division each chromosome splits lengthwise and a half of every one goes to either new cell.

Each species has a definite chromosomal complex, the characteristics of which are most readily distinguished just before the halves of the chromosomes separate during cell division. For instance, the number of chromosomes is practically constant, although certain exceptions exist due to the sex-determining mechanism, supernumeraries and multiple formation. Also a graded size series is usually present. This series is actually double as there are almost invariably two of a given size and shape. Of these two morphologically alike, paired or homologous chromosomes, one has been derived from the male and the other from the female parent.

The germ cells in preparation for fertilization undergo a series of changes called collectively gametogenesis. The part of this process with which we are particularly concerned is called maturation and consists of two cell divisions of a somewhat special type. These are known as the first and second maturation divisions. The behavior of the pairs of chromosomes during these two divisions is the especial field of this paper.

Before the maturation divisions, homol-

ogous chromosomes conjugate. Each member has already split longitudinally as for an ordinary division so that the result is a chromosome called a tetrad, composed of four parts or chromatids, which may or may not be distinguishable entities. At the first maturation division every first spermatocyte, or oöcyte, as the case may be, gives rise to two cells, each of which contains the same number of chromosomes as its parent cell, but instead of four parts, each chromosome now has two, and is called a dyad. At the second maturation division in the male both of the cells derived from one first spermatocyte divide, giving four cells (spermatids) in all. Each of these cells contains one chromatid from every tetrad; e.g., if a first spermatocyte had 11 tetrad chromosomes, each of the four spermatids to which it gave rise would have 11 chromosomes but every one of the latter would be a single chromatid or monad, as they are now called. The oöcyte goes through a similar process but only one functional egg is formed, as three of the cells are abortive. In either case the germ cells become haploid, that is, they contain a single series of chromosomes. The union of the two mature germ cells to form a new individual restores the full, or diploid, number of chromosomes. Thus the initial reduction in number of chromosomes occurs through the union (synapsis) of homologous or like chromosomes, one contributed by the egg and one by the sperm, and not as a result of cell division. This process is known as pseudo- or false reduction, since the actual distribution to different cells is accomplished by the two following divisions.

The question of interest is—Which division separates the part of a tetrad derived from one parent from that derived from the other? Obviously, there are several

possibilities. The synapsed pairs may separate at the first division; one-half of each may go into either second gametocyte to be separated at the second division; or, it may be a matter of chance whether the dyads which separate at the first maturation division are derived from the same or opposite parents. Do all of the tetrads of a species follow a given procedure? Or, may the tetrads differ in this respect among themselves? Or, finally, do the homologues of a particular tetrad segregate, for example 90 per cent of the time in one division while those of another tetrad segregate 25 per cent of the time, and if so, what is the cause of this differential behavior? Let us first view the matter from a historical standpoint, then consider the facts presented by recent work.

II. HISTORICAL BACKGROUND

Cytology, in so far as it deals with the chromosomes and heredity, really began in 1883, forty-three years ago, with Van Beneden's discovery that egg and sperm of *Ascaris megalocephala* each contribute one-half of the chromosomes found in the somatic cells of the species. He also saw that this reduction in amount of chromatin in the germ cells occurred at maturation. He assumed that the egg cast out the chromatin which had been brought in by the sperm and the sperm that which it had received from the egg. According to this hypothesis the germ cells alone would be truly male or female and all individuals that resulted from their union would be hermaphrodites. His conclusions have been shown to be erroneous but his observations stand.

In the same year Roux advanced his hypothesis of the linear arrangement of chromatin which is qualitatively different in various regions of the chromosomes.

In 1888 Strasburger reported that Van Beneden's observations applied to a number of flowering plants and a year earlier Flemming, Carnoy and others had shown similar conditions to prevail in other animals.

Flemming ('87) recognized a difference in the appearance of chromosomes in the two maturation divisions. In the second of these he saw that the chromosomes resembled those of an ordinary mitosis, and hence he called it a *homeotypic* division. He also observed that the chromosomes of the first were different and called this division *heterotypic*. Unfortunately, most of the later writers have considered the heterotypic and reduction divisions as synonymous. Flemming's description did not involve this association but it has become so firmly established as to render the use of the terms heterotypic and homeotypic undesirable.

As a matter of fact the chromosomes of the second maturation division resemble those of an ordinary mitosis because they are identical in structure. In each case, a chromosome at metaphase is composed of two similar parts or chromatids. The chromosomes at the first maturation division, on the other hand, are actually composed of four similar parts or chromatids, whether or not they are visible, hence the appearance is different. The two chromatids which go to each cell at the first division may be derived from different parents or may be each one-half of a parental chromosome: as will be shown later, unless there is a morphological or physiological difference between the homologues it is impossible to determine which is the case.

Weismann in 1887, in an essay based on Roux's work of 1883, put forward what is now known as the Roux-Weismann hypothesis which holds: (1) the chromatin

is the physical basis of heredity; (2) it is differentially organized; and (3) the differentiated units are linearly arranged. In order to maintain a constant number of "ids," Weismann saw that reduction of number must occur before fertilization; otherwise, the number would be doubled at each generation. He predicted that reduction would be found to occur during maturation and that one of the divisions would be distinguishable in form from the other. He suggested two ways in which this reduction might occur, either by a sorting out of chromosomes into two similar groups, one of which would go to each pole without division of the constituent chromosomes, or by a transverse instead of a longitudinal division of each individual chromosome. For the intrinsic process, whatever the method, he proposed the term *reduction division*. The ordinary longitudinal division was already known as an *equation division*.

This paper appeared simultaneously with that of Flemming in which he described the first maturation division as heterotypic.

We have then these facts established; (1) the body cells and unripe germ cells of most organisms contain twice as many chromosomes as the mature germ cells; (2) the reduction in number is effected during maturation, and (3) the diploid number is restored by the union of the germ cells to form a new individual. The foregoing presupposes that the chromosomes are self-perpetuating bodies which grow and reproduce themselves, but never lose their individuality although, of course, they may change their appearance.

Van Beneden's report ('83) that egg and sperm of *Ascaris megalocephala* each contribute one half of the chromosomes which are present in the cells of the early embryo contained the inherent idea of a

persistent individuality. Rabl ('85) was the first, however, to definitely study the chromatin in its diffused condition in order to determine the behavior of the chromosomes in the formation of the so-called nuclear network. He concluded that the chromosomes preserve not only their identity but largely the grouping which they had at the end of the preceding division. While the chromosomes do form fine anastomosing branches which give the appearance of a network, critical study of the conformation of such a nucleus revealed the areas occupied by individual chromosomes and that during condensation the chromatic substance contracted and the chromosomes assumed definite form again in approximately the same position which they had occupied at the beginning of the process. Rabl's paper was based on his study of the body cells of *Salamandra maculata* (Rabl) and still deserves to rank as a masterpiece of early cytological literature along with those of Flemming, Van Beneden and Boveri. However, the clean cut and persistent work of Boveri, from 1888 on for a number of years, did most to establish the concept of chromosome individuality. Thus the foundation for the chromosome theory of heredity was laid within the five year period from 1883 to 1888.

Much of the work since has been concerned with the manner and time of reduction. Almost every conceivable mechanism has been sponsored at one time or another. According to Weismann's hypothesis each chromosome was composed of ids, and each id contained determiners for the sum of all the characters of the organism. The chromosomes, therefore, would differ from one another only in so far as there was variation in a species since they would represent different lines of ancestral germ-plasm. Even many of the early cytologists agreed

with this view that the chromosomes were essentially alike both qualitatively and quantitatively.

III. MORPHOLOGICAL AND PHYSIOLOGICAL DIFFERENCES BETWEEN CHROMOSOMES DEMONSTRATED

Three papers which appeared in 1901 and 1902 undermined this view. Two of these, one by Boveri and the other by McClung, strongly indicated functional differences. The other by Sutton clearly demonstrated morphological distinctions.

Boveri studied the larvae of sea-urchins in which the normal combination of chromosomes had been altered by means of double fertilization. He found 36 chromosomes in the normally fertilized eggs of the species with which he worked, 18 of which were contributed by each parent. Eggs which had received two sperm had another set of 18, which gave 54 chromosomes. When these had split for the first cleavage there were 108. Double fertilized eggs usually formed four, or occasionally three, cells (blastomeres) at the first cleavage. If the chromosomes happened to be distributed equally in the case of four cells each would receive 27, which would be less than the normal number, 36. As a matter of fact they were not distributed equally. Some cells received more than 36, others correspondingly less. Normal embryos appeared very rarely. As Boveri knew from experiments with enucleate fragments of egg and artificial parthenogenesis that the reduced set of chromosomes contributed by the sperm or egg alone was sufficient to cause normal development, he concluded that each blastomere formed by the first cleavage of these "normal" larvae had received at least one complete haploid set. In such larvae all of the parts were present and fully developed but different thirds

or fourths showed individual variations which normally could be found only in different specimens. Ordinarily the plutei were not normal but the different thirds or fourths could be recognized as coming from a given one of the original blastomeres. One part would be normal for example, as regards skeletal development, while others would lack any trace of a skeleton. Furthermore, it was known that the first four cells formed by cleavage might be separated from each other and that such isolated blastomeres from a normally fertilized egg developed exactly alike while those from a doubly fertilized egg very rarely did.

From these facts Boveri concluded, to translate literally, that: Not a given number but a given combination of chromosomes is necessary for normal development and that this can mean nothing else than that the individual chromosomes must possess different qualities.

McClung had previously reported the occurrence in the Orthoptera of one chromosome, called the accessory, which differed from the others during spermatogenesis both in behavior and in distribution in such a manner that half of the mature sperm possessed and half lacked this chromosome. In 1901 he put forward his hypothesis that this chromosome was a sex-determinant and thus for the first time suggested an association between a particular chromosome and a particular character or group of characters.

Shortly afterward Sutton ('02) published his critical analysis of the morphological characters of the chromosome group of the short-horned grasshopper, *Brachystola magna*. He showed that the diploid group of twenty-three was made up of two morphologically equivalent size series of eleven members each with one additional chromosome, the accessory. There were six smaller chromosomes and

seventeen larger ones; but except for the accessory there were always two of a size. In the first spermatocyte, he found that each two of a given size had united so that the haploid number of chromosomes formed a single size series. The six small ones had paired to form three small tetrads; likewise, sixteen of the larger ones had united in pairs, leaving the accessory without a mate. In the second spermatocyte, where the chromosomes again were dyads as in the spermatogonia he readily recognized a single haploid series directly comparable to either of the size series of the spermatogonia. As this was the last division before fertilization and the egg was known to undergo a similar process, Sutton readily concluded that the other size series was contributed by the egg.

As his final suggestion in this paper Sutton wrote: "I may finally call attention to the probability that the association of paternal and maternal chromosomes in pairs and their subsequent separation during the reduction division as indicated above may constitute the physical basis of the Mendelian law of heredity"; this view he elaborated a year later and it has since received support from many lines of work.

These three contributions by Boveri, McClung and Sutton firmly establish the concept that the chromosomes differ both quantitatively and qualitatively.

IV. GENETICAL EVIDENCE OF QUALITATIVE AND QUANTITATIVE DIFFERENCES BETWEEN CHROMOSOMES

The confirmation of these views by combined genetical and cytological studies is too well known to need much discussion. Two of the best known instances of such correlated studies are those on the fruit-fly, *Drosophila*, by Morgan and his group at Columbia, and on the

Jimson weed, *Datura*, by Blakeslee and Belling at Cold Spring Harbor.

In *Drosophila melanogaster* the diploid chromosomal complex consists of two large pairs, one small pair and the sex chromosomes, xy in the male and xx in the female. From genetical studies the behavior in heredity of some hundreds of characters is known. These characters fall into four groups, a large one which is sex-linked and where the characters follow the same sort of distribution as the sex chromosomes, one small group known to be associated with the small pair and two large non-sex-linked groups which correspond to the two large pairs.

In the Jimson weeds, the haploid complex consists of twelve chromosomes, but Blakeslee and Belling have obtained plants which instead of being diploid are triploid; that is, they have three complete sets of chromosomes. During maturation two of the three chromosomes of a set go to one pole and one to the other, the distribution of the different sets taking place at random. The gametes, therefore, contain various different combinations, so that on recombination during fertilization it is possible to get various assortments. By patient work, Blakeslee, Belling and their associates have sorted out twelve mutants, each of which has a different set of chromosomes in the triploid condition, while the other chromosomes are present in the normal diploid sets. It is possible to know their chromosomal constitution from a superficial study of these mature plants.

V. OPPONENTS OF THE CHROMOSOME THEORY OF HEREDITY AND THEIR THEORIES

Notwithstanding such clear cut support for the chromosome theory of heredity, a certain group of workers have been ready to take the opposite side of the argument; that is, they are sceptical as

to the chromosomes preserving their individuality from one cell generation to another or even having individuality at any time. Likewise, they are not willing to grant that the chromatin is the physical basis of heredity. Meves, Fick and Della Valle are among the leading opponents of the chromosome theory of heredity and their views may be mentioned briefly.

Meves ('96, '11) holds that each species inherits the capacity to produce a given number of chromosomes from the chromatin of the resting nucleus of the body cells and to form half that number in the germ cells at maturation, just as it inherits the ability to develop other characters belonging to the species.

According to Della Valle ('11), the chromosomes arise *de novo* from the resting nucleus after the manner of the formation of liquid crystals, their size being due to a physico-chemical quality of the chromatin and their numbers to the quantity of chromatin present. This theory does not account for the fact that the chromosomes, at their maximum density within the cell, attain various sizes in most species, nor does it explain why the gametocytes, the nuclei of which are much larger than any others in the body, should have only half as many chromosomes.

Fick ('05) has a similar conception which he has advanced as the "Manoeuvrierian hypothesis;" he claims that the chromosomes which appear at each cell division are *de novo* "tactical formations" of the chromatin comparable to the manoeuvres of a military body. The force which is assumed to direct these manoeuvres is again a physico-chemical one.

The objection to such hypotheses is that they do not fit the facts. For a discussion of the subject the reader is referred to papers by Wilson ('09, '10), McClung ('17), and Parmenter ('19).

VI. VARIOUS THEORIES AS TO SYNAPSIS
AND SEGREGATION OF HOMOLOGOUS CHROMOSOMES

Let us return to a consideration of the work of those who regarded the chromosomes as persistent and self-perpetuating physical entities.

Rückert ('92) and others held that the chromosomes before any cell division, greatly elongated into fine, coiled threads which became associated end-to-end to form a continuous spireme. In the case of ordinary cell division this spireme segmented into the diploid number of chromosomes, but at the time of maturation it segmented into the haploid number. During the first maturation division, the chromosomes were supposed to divide in the same manner as in the body cells, i.e., by means of a longitudinal split. The second division was held to be transverse so as to reduce the number of different ancestral germ-plasms, used in Weismann's sense. Weismann himself expected reduction to occur at the second maturation division because the diploid number of chromosomes was known to be present in certain parthenogenetic eggs which form but one polar body.

O. Hertwig ('90), Boveri ('89), and Brauer ('93), were among the first to report that the chromosomes are split twice longitudinally as they enter the maturation divisions. For this reason they at first denied the existence of a reduction division which, under the conception of the time, seemed to involve a transverse division. However, the work of Winiwarter ('00), the Schreiners ('06) and others made it apparent that only one of the spaces was due to a split, while the other was the space between the members of a pair that were associated side-by-side instead of end-to-end. Thus, they clearly showed that a reduction di-

vision in Weismann's sense would be one which separated the parts derived from different parents.

Some assumed that two separate spiremes were formed, each by the end-to-end union of the chromosomes derived from a given parent. These spiremes first split, then conjugated side-by-side, and finally discontinued the end-to-end association so as to leave the haploid number of chromosomes (tetrads); the four parts of each of these were separated longitudinally in planes at right angles to each other. Others, chiefly Vejdovsky ('07) and Bonnevie ('08) believe that the chromosomes completely fuse longitudinally and that the resulting body then splits twice lengthwise so as to give four equal parts which, however, are not comparable to the halves of the conjugating chromosomes.

The view most generally held at present is that no continuous spireme is formed but that the homologous chromosomes unite. According to some, the association is end-to-end (telosynapsis); to others, side-by-side (parasynapsis). While both types of synapsis may exist it is significant that parasynapsis has usually been reported wherever the stages which directly follow the last spermatogonial or oögonial anaphase have been studied in detail from favorable material.

A. and K. E. Schreiner ('06) presented the first convincing support of this view in their work on the annelid, *Tomopteris*. Wenrich ('16) published one of the most authoritative pieces of evidence for parasynapsis. In *Phrynotettix magnus*, a short-horned grasshopper, he was able to trace three well marked pairs of chromosomes from the spermatogonia through the growth period to the first maturation division.

Both McClung and Robertson were at first led to favor telosynapsis by their

studies of prophases of the first spermatocytes of short-horned grasshoppers, but changed their views when they carried their studies back to the more difficult stages which immediately follow the last spermatogonial division.

Among the most ardent advocates of an end-to-end union today are the *Oenothera* cytologists, Davis, Gates and Cleland. In every figure which they have published it is granted that dyads are in end-to-end union; but these figures all represent stages which just precede the first maturation division—and this is exactly the phase which at first led McClung and other competent cytologists to favor telosynapsis, even in a group as exceptionally favorable for cytological work as the grasshoppers. There is not one satisfactory figure of the stages which immediately follow the last pre-maturation division.

On the other hand, since 1904 Gregoire has consistently argued for parasynapsis in the flowering plants, and no case of telosynapsis can be considered as satisfactorily demonstrated by studies on material fixed in such a manner as to give the artificial clumping of chromatin in a more or less solid mass at one side of the nucleus, known as synizesis. Such a fixation renders it impossible to study the very stages at which parasynapsis would be expected to occur. The later end-to-end association may be only the final stage of disunion between chromosomes which were originally synapsed side-by-side.

Both types of synapsis may occur, but as we shall see presently, the question of the occurrence of either type is immaterial in a determination of time of segregation. In the meanwhile, let us orient ourselves by consideration of some general questions.

VII. GENERAL QUESTIONS INVOLVED

In the first place, what is the object of synapsis? The purpose which first appealed to me as self-evident is fully expressed by the following quotation from one of Sutton's papers ('02, p. 39): "There is, therefore, in *Brachystola* no qualitative division of chromosomes but only a separation of the two members of a pair . . . by the light of this conception we are enabled to see an explanation of that hitherto problematical process, synapsis, in the provision which it makes that the two chromosomes representing the same specific characters shall in no case enter the nucleus of a single sperm or mature egg." This still seems to me the basic necessity back of synapsis. The phenomenon known as crossing-over occurs during the process, either by means of chiasmata or otherwise, but this, in my opinion, is an incidental result rather than a fundamental purpose.

The next question which logically presents itself concerns the necessity for two maturation divisions; if the preceding assumption is correct, one would evidently be sufficient for the purpose of segregation. I would suggest that the occurrence of an extra division is perhaps simpler than an alteration in the very mechanism of division. At a given stage of mitosis, probably the telophase, the chromosomes normally split in anticipation of the next division with the result that each member of a pair is already split before they synapse. It would seem that this normal split would have to be suppressed or two divisions must take place to distribute the four parts present after synapsis. On the basis of this explanation, another split might be expected during the telophase of the first maturation division. However, the chromosomes are already dyads

and this condition may be sufficient to inhibit a further splitting.

Finally, we may be asked why we are concerned as to which division separates homologues, especially since the two divisions distribute each of the four chromatids of a tetrad to different germ cells. For a dyed-in-the-wool scientist, a satisfactory answer is that we desire to know the truth. For those who have never known the thrill of establishing a scientific fact, there is also a sufficient answer. Since the chromatin is now generally accepted as being the physical basis of heredity, it is clearly desirable to determine as accurately as may be its behavior during maturation and fertilization since only with accurate knowledge of the usual behavior is it possible to detect variations which may be, in part, the mechanism of evolution, and to determine experimentally, if not the causes which operate in nature, at least others which will produce effects. Among the more drastic measures with which the laboratory worker is inclined to experiment may be mentioned radium, X-rays and alcohol. Others which approach nearer the experiments of nature seem to me to be more likely to render significant results. Chief among these is an enforced change of food habit, such as a drought or accidental landing in a new habitat might cause. In the light of our present knowledge of various vitamins, calcium metabolism, etc., this seems one of the most promising lines of work. Experiments with extremes of humidity and temperature may also be expected to yield results.

Any cause which will produce an effect on the chromatin of the germ cells such as a permanent multiple association, a shift of spindle fiber, or a change in the size of a chromosome (all of which are known) or some less tangible effect which

may cause segregation at one division rather than another may be expected to produce physiological as well as morphological changes. If these are produced for a single season in any considerable portion of a population they will perpetuate themselves provided they are not detrimental, for this is not a question of inheritance in the usual sense, but of actual physical transmission.

VIII. DIRECT EVIDENCE AS TO THE TIME OF SEGREGATION

Let us next consider the facts in regard to the time of segregation. Obviously, given a side-by-side union of morphologically similar, split homologues, it is quite impossible to tell which two of the four threads have come from a given parent. This is especially true because the larger pairs form 8-shaped figures in which the strands are separated two-by-two in planes at right angles to each other in such a manner that the threads which are together in one loop are apart in the next (fig. 1, *A*). Even the smallest tetrads pass through a stage where the four chromatids are arranged in the form of a cross with equal arms (fig. 1, *B*), while some develop modified ring and cross forms (fig. 1, *C* and *D*). Such figures as these are typical of the late prophase preceding the first maturation division in both animals and plants, though they have frequently been misinterpreted. The unprejudiced reader, I am sure, will readily admit that it would not be possible in any of these instances to say which two of the four chromatids of any one of these tetrads has been transmitted by the mother and which two by the father. Yet most cytologists whose work has dealt with these stages have taken sides in favor of either pre-reduction (segregation at the first) or post-reduction (segregation at the second

maturation division). The conclusions in practically every instance have been based on attempts to distinguish between the space which results from a longitudinal cleavage of the chromosomes and that which separates the synapsed members.

As might be expected, the attempt to determine the facts by such uncertain means has not resulted in agreement. Some of the advocates of telosynapsis have favored pre-reduction [notably Montgomery ('01), Farmer and Moore ('05)

for forms like that represented at figure 1, *D*, but it is not so convincing when we consider figure 1, *A*, where the chromatids which are together in one loop (*a*) are clearly separate in the next (*b*). Wenrich ('16) was the first to take the position that either pre- or post-reduction may follow parasynapsis.

As already indicated, Wilson and McClung argued for telosynapsis and post-reduction in their earlier papers. Later they became convinced that parasynapsis is at least the most usual method of

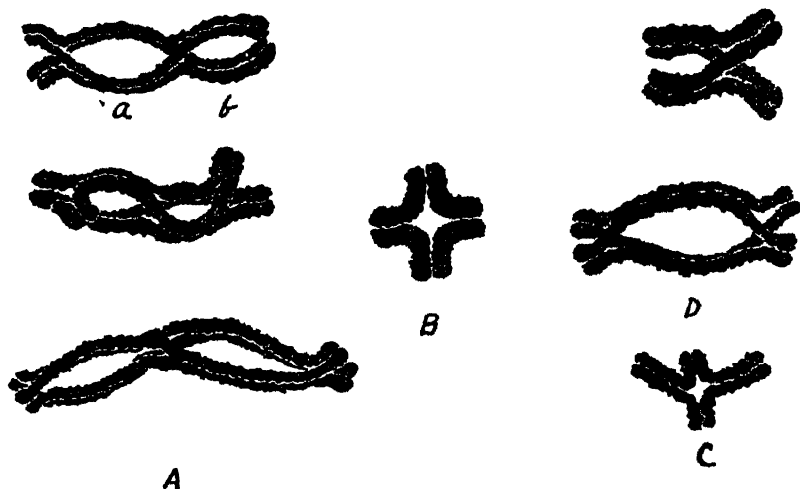


FIG. 1. TYPICAL TETRAD FORMS FOUND IN THE PROPHASE OF THE FIRST MATURATION DIVISION

Note the four parts (chromatids) of each. (From camera lucida drawings of first spermatocyte prophases of three species of grasshoppers.)

and the present *Oenothera* cytologists] others post-reduction (see the papers prior to 1912 of McClung, Sutton and Wilson). The adherents of parasynapsis have shown more unanimity in support of pre-reduction [Winiwarter ('00), Gregoire ('07), the Schreiners ('08), Janssens ('09) and Robertson ('16)]. In general they have assumed that the chromatids open out along the space between the homologues more readily than along the plane of the longitudinal cleavage. Such a view might seem logical

union and that it is impossible to determine which division is equational and which is reductional from a study of the relations of morphologically similar chromatids.

Fortunately considerable direct evidence is available from several sources. (1) *Heteromorphic homologues*. Homologues occasionally differ morphologically. In such cases, it is only necessary to obtain individuals in which the members of a pair are heteromorphic and study the distribution of the parts of the resulting

tetrads during the two maturation divisions. (2) *Dyads (except sex-chromosomes) present at first maturation division.* Dyads may be present either as a result of the failure of homologues to conjugate or on account of an upsetting of normal conditions such as occurs in *Datura*. (3) *Sex-chromosomes.* These may be either an X-Y pair, the members of which are morphologically different, an unpaired X or accessory chromosome or a hexad multiple. (4) *Genetical evidence.* In certain species of *Sphaerocarpus* the four spores formed by the division of a spore mother cell remain together at maturity. Allen has demonstrated that the sex determining mechanism is an X-Y pair and has obtained evidence as to the time of segregation in clones derived as above through studies of the mode of inheritance of a pair of characters, the determiners for which are carried by another pair of chromosomes.

(1) *Heteromorphic homologues.* The heteromorphism between homologues so far reported has been of three types: (a) difference in size, (b) difference in point of spindle fiber attachment and (c) difference in contour due to constriction.

(a) The first of these to be reported was a size difference between homologues in three species of short-horned grasshoppers (Carothers, '13). In this group there are twelve pairs of chromosomes in the female and eleven pairs and one without a mate (the accessory or sex-chromosome) in the male. It is customary to number these pairs from one to twelve beginning with the smallest. To date, size differences between homologues have been reported for the first four pairs. The individuals belong to nine genera though it would be possible to greatly extend this number by working over the material in the McClung collection.

My own work, to which reference was just made, dealt with the second pair in one species and the third pair in the other two. Certainly in a vast majority of the cases, segregation occurred at the first maturation division. Robertson ('15) reported a similar condition and behavior in two other species; in one of these, the first pair was involved, in the other the fourth. Neither Robertson nor myself were primarily interested in the time of segregation and it is quite possible, in my own work at least, that occasional segregation at the second division may have been overlooked. However, a later, somewhat hasty review of the slides on which my work was based failed to reveal any case of post-reduction of the members of the unequal pair, so, in table 1, I have recorded these five instances as giving 100 per cent pre-reduction.

Wenrich ('16) in a very detailed study of the spermatogenesis of thirteen specimens of *Phrynotettix magnus*, another short-horned grasshopper, found two small pairs. One, which he designated as "B," had homologues differing in size in eleven out of the thirteen animals. Unlike the five preceding instances, the homologous members always segregated at the second division. The other small pair, which he called "C," was composed of unequal homologues in seven of the thirteen specimens. Furthermore, two types of inequality were present. One type, "C₁," occurred in five individuals and, as in the case of pair "B," the members always segregated at the second division. The other type "C₂," was present in two of the animals and a count of 92.8 first spermatocyte metaphases chosen at random gave 50.8 per cent pre-reduction and 49.2 per cent post-reduction.

The study of this subject has been extended to species in three other genera

by the writer in a paper ready for press. Certain individuals in all of these have one or both of the two smaller pairs composed of unequal homologues (11 out of 71 *Trimerotropis citrina* for the second pair). *Amphitornus bicolor* gives over 99 per cent post-reduction for the homologues of both pairs. *Mecostethus gracilis* gives 78 to 80 per cent post-reduction for

reduction, and one 50 per cent pre-reduction and 50 per cent post-reduction. Evidently, segregation occurs with about equal facility at either division, but a given pair in a particular species behaves in a predictable manner.

(b) *Heteromorphism due to shift of spindle fiber attachment*. Chromosomes throughout the plant and animal kingdom are of

TABLE 1
Time of segregation

	1ST PAIR		2ND PAIR		3RD PAIR		4TH PAIR		J TETRADS		HEXADS		ACCESSORY		X-Y	
	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd
	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent	per cent
<i>T. citrina</i>	95	5	10	90												
<i>M. gracilis</i>	20	80	22	78												
<i>A. bicolor</i>	1	99	1	99												
<i>P. magnus</i> C ₁	50	50	0	100												
<i>P. magnus</i> C ₂	0	100														
<i>A. granulata</i>	100	0														
<i>A. simplex</i>			100	0												
<i>B. magna</i>					100	0										
<i>D. carolina</i>					100	0										
<i>T. parvipennis</i>							100	0								
<i>Trimerotropis</i>									100	0						
<i>Circotettix</i>									100	0						
<i>Marmiria</i>											100	0				
<i>Hesperotettix</i>											100	0				
<i>Anabrus</i>											100	0				
<i>Acrididae</i>													100	0		
Bugs { <i>Anasa</i>													0	100		
<i>Banusa</i>													100	0		
20 species.....													100	0		
8 species.....													0	100		
20 species.....															100	0
13 species.....															0	100

both pairs and correspondingly 20 to 22 per cent pre-reduction. *Trimerotropis citrina* shows 95 per cent pre-reduction for the first pair and 90 per cent post-reduction for the second.

Thus, out of fourteen pairs of chromosomes with homologues which differ in size, six show 95 to 100 per cent pre-reduction, seven 78 to 100 per cent post-

reduction, and one 50 per cent pre-reduction and 50 per cent post-reduction. Evidently, segregation occurs with about equal facility at either division, but a given pair in a particular species behaves in a predictable manner.

(b) *Heteromorphism due to shift of spindle fiber attachment*. Chromosomes throughout the plant and animal kingdom are of

ment. The only exceptions, so far reported, are found in certain species confined to two genera of grasshoppers. A combined genetical and cytological study of one of these species, *Circorettix verraculatus* (Carothers, '21), demonstrated that the point of fiber attachment is constant from parent to offspring. In this species, three pairs of chromosomes may be heteromorphic. They are numbers one, seven and eight. Of course, the presence of a heteromorphic pair in one individual presupposes the existence of other individuals in which the homologues would be homomorphic. This becomes clearer on examination of figure 2, which summarizes the results obtained from five matings so far as the three potentially heteromorphic pairs are concerned. The three vertical groups numbered 8, 7 and 1 correspond to the pairs of chromosomes under consideration. The numbers on the left margin indicate the mating. The chromosomes of the male parent are represented on the left of each group, those of the female next, and finally the numbers of male offspring obtained and the various chromosomal recombinations shown by them. If we partly analyze mating number 14, for example, we see that both parents were heteromorphic for the eighth pair. They would both, therefore, form two types of gametes so far as this pair of chromosomes is concerned. In one type it would be present as a rod, in the other as a V. Chance union of these gametes would give the well known Mendelian dihybrid ratio, 1:2:1. The numbers actually obtained, two homomorphic for Vs, six heteromorphic and four homomorphic for rods, approximate this ratio as closely as could be expected from a family of this size. This text-figure is reproduced from my 1921 paper at the cost of some digression since it has a bearing on several

points discussed in the present paper. Among these is the persistent identity of chromosomes from parents to offspring, the segregation of the members of a pair into different gametes and their recombination in the offspring according to the laws of chance.

Heteromorphic pairs like these where the difference is one of spindle fiber insertion, always, so far as known, segregate at the first maturation division. I am inclined to think that the reason for this is to be found in the mechanical conditions involved. Certainly it does not follow that when the homologues are homomorphic of either type (Vs or rods) they also segregate at the first division. We have already seen that rod-shaped homologues run the complete scale of possibility as to time of segregation and there is no reason for supposing that those which are V-shaped do not behave in a similar manner.

(c) The third type of heteromorphism mentioned, that due to a constriction, is represented in mating number 2 by one homologue of the seventh pair in the female and is also present in her one male offspring. Such a homologue when associated with either a rod or V-shaped mate always undergoes pre-reduction.

(2) *Dyads (except sex-chromosomes) present at first maturation division.* The unequal homologues of the second pair in *T. citrina* occasionally fail to synapse or else separate so precociously that they lose all orientation in regard to each other by the time of the first maturation metaphase. At all events, they enter this stage not as a tetrad but as two dyads, and their ensuing behavior appears to be purely a matter of chance. They may pass to the same pole or to opposite poles without division: or, either one may divide and the other pass to one pole undivided; giving, in effect, a reduction

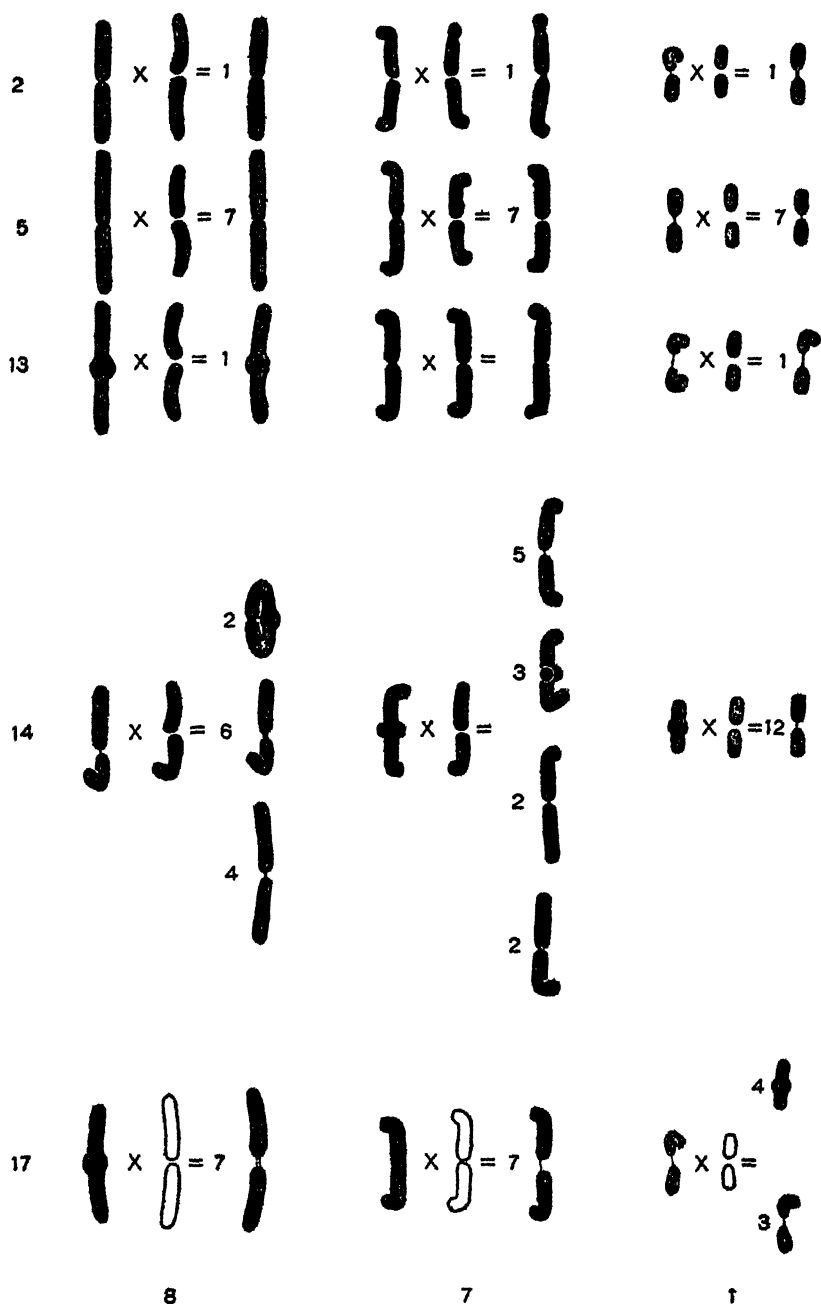


FIG. 2. *Circotettix verruculatus*. A CONDENSED ARRANGEMENT SHOWING THE MORPHOLOGY OF THE THREE CRITICAL PAIRS OF CHROMOSOMES IN THE PARENTS OF EACH OF FIVE MATINGS AND THEIR MALE OFFSPRING WITH THE NUMBER OF INDIVIDUALS IN EACH CLASS

The chromosomes of the male are represented on the left; those of the female on the right. In mating no. 17, where the form of the chromosomes of the female can only be hypothesized, they are represented in outline.

division for one and an equational division for the other: or, both may divide. In the last case and all others where they enter the second maturation division as monads they do not divide again but simply pass to one pole at random. This erratic behavior lends point to the suggestion made in the earlier part of this article that synapsis is primarily for the purpose of insuring the distribution of one chromatid of every tetrad to each mature germ cell; and it also appears that the two maturation divisions act as a unit process to secure this result, rather than that either one is especially for the purpose of segregation.

On the other hand, in the *Oenothera* and *Datura* mutants where the normal complex has become unbalanced, the extra dyads are reported to segregate uniformly at the first division. To demonstrate that such behavior is invariable would require a rather extensive study.

(3) *Sex-chromosomes*. McClung ('01, '02) put forward a hypothesis of sex-determination which is now generally accepted. The chromosomal mechanism on which this hypothesis was based may be made clear if we consider its operation in the short-horned grasshoppers. The males in this group have twenty-three chromosomes, eleven pairs and the unpaired accessory or sex-determinant. The females have twenty-four chromosomes, twelve pairs. (The accessory has a mate in this sex). After maturation the eggs all contain twelve chromosomes; the sperm on the other hand are of two sorts, one with eleven chromosomes and the other with twelve. The union of one of the latter with an egg results in a complex of twenty-four chromosomes, and the egg develops into a female, while fertilization with a sperm bearing eleven chromosomes gives a group of twenty-three chromosomes, and a male is produced.

At the first maturation division in the male, each of the eleven tetrads divides, the accessory passes into one of the resulting cells without division. In effect this is pre-reduction for the accessory chromosome and results in two types of second spermatocytes, one with eleven dyads and the other with twelve. During the second maturation division each of these cells gives rise to two of its own type except that the chromosomes are now monads instead of dyads.

The hexad multiples are formed by the union of the accessory with one homologue of an ordinary pair and always undergo pre-reduction.

The squash bugs, also, have an unpaired accessory in the male but it divides at the first maturation division along with the tetrads so that all the second spermatocytes are alike. During the second maturation division the dyads separate to form monads but the accessory is already a monad, hence, it passes into one of the daughter cells without division, so that, as in the grasshoppers, two types of sperm are formed but in this instance the accessory undergoes post-reduction.

In many organisms there is a slight modification of this sex-determining mechanism where the accessory has a synaptic mate (Y) in the male. The two are morphologically distinct and are known as the X-Y pair. The end result is again two types of sperm, one bearing Y, which is male-producing, and one bearing X, which is female-producing. The X-Y pair, also, may undergo either pre- or post-reduction. Wilson in his recent book lists forty species, extending from insects to mammals, reported to have an unpaired accessory, which undergoes pre-reduction in thirty-two of the species, and post-reduction in eight, while of thirty-three species having an X-Y pair

pre-reduction is reported for twenty- and post-reduction for thirteen.

The recent work on sex-chromosomes in plants is not yet extensive enough to justify comparisons as to time of segregation.

(4) *Genetical evidence.* Botanical cytologists have stood almost as a unit in favor of pre-reduction; it is, therefore, of especial interest that Allen ('24) was forced by his genetical work on *Sphaerocarpos* to the conclusion that the most reasonable inference from his facts was, "that in some way qualitative segregation can be brought about in both divisions." A clear presentation of his facts would require considerable space and anyone sufficiently interested can acquire them from the original paper.

From the foregoing facts it is evident that neither maturation division can rightly be called a segregation, or reduction, division. The members of a given pair may possess a tendency to segregate at one division in preference to the other,

but this is seldom a fixed condition. The two maturation divisions are essentially a unit process and segregation may occur in either.

My hope in presenting this article is (1) that the public may gain a clearer conception of the fundamental principles involved in the process of maturation; (2) that cytological workers will be deterred from making definite statements that either pre- or post-reduction occurs in the material with which they happen to be working unless it is possible to identify the contribution of the two parents for each particular pair of which they speak; and, finally, (3) that teachers will grasp the idea that the maturation divisions are really a unit, and cease to tell the much-abused freshman that one maturation division is for the purpose of segregation and the other is superfluous.

(I am greatly indebted to Dr. H. B. Baker and to Dr. D. H. Wenrich for valuable criticism of this manuscript.)

LIST OF LITERATURE

- ALLEN, C. E. 1924. Inheritance by tetrad sibs in *Sphaerocarpos*. *Proc. Amer. Phil. Soc.* 63: 222-235.
- BELLING, J., and BLAKINLEE, A. F. 1922. The assortment of chromosomes in triploid *Datura*. *Amer. Nat.* 56: 339-346.
- BLAKINLEE, A. F. 1922. Variations in *Datura* due to changes in chromosome number. *Ibid.* 56: 16-31.
- BONNEVIE, K. 1908. Chromosomen Studien. 1. *Arch. Zellf.* 1: 450-514.
- BOVERI, T. 1887. Über die Befruchtung der Eier von *Ascaris megalocephala*. *Sitzber. Gesell. Morph. Phys. München* 3.
- . 1902. Über mehrpolige Mitosen als Mittel zur Analyse des Zellkerns. *Verhandl. Phys. Med. Ges. Würzburg*, 35.
- BRAUER, A. 1893. Zur Kenntniss der Spermatogenese von *Ascaris megalocephala*. *Arch. Mikr. Anat.* 42: 153-212.
- CAROTRERS, E. ELEANOR. 1913. The Mendelian ratio in relation to certain Orthopteran chromosomes. *Jour. Morph.* 24: 487-511.
- . 1921. Genetical behavior of heteromorphic homologous chromosomes of *Circotettix* (Orthoptera). *Jour. Morph.* 35: 457-483.
- DILLA VALLE, P. 1911. Le analogie fisico-chimiche della formazione e della dissoluzione dei cromosomi. *Monitore Zool. Ital.* 22.
- FARMER, J. B., and MOORE, J. E. S. 1905. On the meiotic phase (reduction divisions) in animals and plants. *Quar. Jour. Micr. Sci.* 48: IV, 489-557.
- FICK, R. 1905. Betrachtungen über die Chromosomen, ihre Individualität, Reduktion und Vererbung. *Arch. Anat. u. Phys. Suppl.* 179-228.
- FLEMMING, W. 1879. Über das Verhalten des Kernes bei der Zelltheilung, etc. *Virchow's Arch.* 77.
- . 1887. Neue Beiträge zur Kenntniss der Zelle. *Arch. f. Mikr. Anat.* 37.
- GRÉGOIRE, V. 1904. La reduction numerique des

- chromosomes et les cinèses de maturation. La Cellule 21: 297-314.
1907. La formation des gemini hétérotypiques dans les végétaux. La Cellule 24: 369-420.
- HERTWIG, O. 1890. Experimentelle Studien am tierischen Ei. Jen. Zeitsch. 17: 1-46.
- JANSSENS, F. A. 1909. La theorie de la chiasmatypie. La Cellule 25: 389-411.
- McCLUNG, C. E. 1901. Notes on the accessory chromosome. Anat. Anz. 20: 220-226.
- . 1902. The accessory chromosome-sex determinant? Biol. Bull. 3: 43-84.
- . 1917. The multiple chromosomes of *Herpotesia* and *Marmira* (Orthoptera). Jour. Morph. 29: 519-605.
- MEVES, FR. 1896. Über die Entwicklung der männlichen Geschlechtszellen von *Salamandra maculosa*. Arch. Mikr. Anat. 48: 1-83.
- . 1911. Chromosomenlängen bei *Salamandra*, nebst Bemerkungen zur Individualitätstheorie der Chromosomen. *Ibid.* 77: 273-300.
- MONTGOMERY, T. H. 1901. Further studies on the chromosomes of the Hemiptera heteroptera. Proc. Acad. Nat. Sci. Phila. 53: 261-271.
- PARMENTER, C. L. 1919. Chromosome number and pairs in the somatic mitoses of *Ambystoma tigrinum*. Jour. Morph. 33: 169-249.
- RABL, C. 1885. Über Zelltheilung. Morph. Jahrb. 7: 289-311.
- ROBERTSON, W. R. B. 1915. Chromosome studies III. Jour. Morph. 26: 109-141.
- . 1916. Chromosome studies I. Jour. Morph. 27: 179-332.
- ROUX, W. 1883. Über die Bedeutung der Kernteilungsfiguren. Leipzig.
- RÜCHERT, J. 1892. Über die Verdoppelung der Chromosomen in Keimblaschen des Salachierlies. Anat. Anz. 8.
- SCHREINER, A. u. K. E. 1906. Neue Studien über die Chromatinreifung der Geschlechtszellen. Arch. d. Biol. 22: 1-70.
- . 1908. Gibt es eine parallele Konjugation der Chromosomen? Erwiderung an die Herren Fick, Goldschmidt und Meves. Vedenskabs-Selskab. Skrif. 1. Math.-Naturv. Klasse 1908, no. 4.
- STRASBURGER, E. 1888. Über Kern- und Zellteilung im Pflanzenreich, nebst einem Anhang über Befruchtung. Hist. Beitrag. 1, pp. 258.
- SUTTON, W. S. 1902. On the morphology of the chromosome group in *Brachystola magna*. Biol. Bull. 4: 24-39.
- VAN BENEDEN, E. 1883. Recherches sur la maturation de l'oeuf, la fécondation et la division cellulaire. Arch. de Biol. 4.
- VEJDOVSKY, F. 1907. Neue Untersuchungen über die Reifung und Befruchtung. Böhm. Gesell. Wiss. Prag.
- WALDEYER, W. 1888. Über Karyokinese und ihre Beziehung zu den Befruchtungsvorgängen. Arch. Mikr. Anat. 32: 1-122.
- WENRICH, D. H. 1916. The spermatogenesis of *Phrynosoma maurus*, with special reference to synapsis and the individuality of the chromosomes. Bull. Mus. Comp. Zool. Harvard Coll. 60: 55-136.
- WILSON, E. B. 1909. Studies on chromosomes V. The chromosomes of *Metapodius*. A contribution to the hypothesis of the genetic continuity of chromosomes. Jour. Exp. Zool. 6: 147-206.
- . 1912. Studies on Chromosomes VIII. Observations on the maturation phenomena in certain Hemiptera and other forms, with considerations on synapsis and reduction. *Ibid.* 13.
- WINIWARTER, H. VON. 1900. Recherches sur l'ovogénèse et l'organogénèse de l'ovaire des mammifères. (Lapin et Homme). Arch. de Biol. 17: 33-199.



ELEVEN THOUSAND GENERATIONS OF PARAMECIUM

By LORANDE LOSS WOODRUFF

Osborn Zoological Laboratory, Yale University

CAN unicellular animals reproduce indefinitely without recourse to fertilization? This was the question to which an answer was sought when the experiment to be summarized was begun nineteen years ago. The consensus of opinion at that time, based chiefly on the work of Bütschli, Maupas, Hertwig, and Calkins, was that fertilization is a *sine qua non* in the life history of the Infusoria (1). The conclusion usually, and I believe rightly, drawn from the data available to-day, largely from the following experiment, is that fertilization plays no indispensable rôle in the life history of Infusoria when subjected to entirely favorable environmental conditions (2). This conclusion, it may be noted, does not deny that fertilization has a stimulating function.

On May 1st, 1907, a pedigree culture of *Paramecium aurelia* was started with a "wild" individual and has been maintained by the isolation of certain of its progeny practically every day, with the exception noted below. The number of divisions has been recorded at each isolation and has afforded a continuous series of data for the study of the reproductive activity of the culture. Throughout the experiment some of the animals discarded from the lines at the daily isolations have been fixed, stained, and mounted as permanent preparations for the study of the cytological changes during the life history. The culture medium for the first eight months of the work consisted of

infusions of hay and fresh grass, but from February, 1908, to the present time various materials collected from ponds, swamps, etc., have been employed. The infusions have invariably been thoroughly boiled to prevent the contamination of the pure culture with foreign strains of *Paramecium*. The possibility of conjugation occurring in the culture has been precluded by the almost daily isolation of the products of division. In short, the animals of the culture today are direct lineal descendants, without fertilization, of the single animal isolated in 1907 (3).

In this manner the pedigree culture was carried for eight years, during which 5071 generations were attained, and then (May 1, 1915), the experiment was considered *formally* closed with the statement that the organisms of the present generation are in as normal morphological and physiological condition as the original individual isolated to initiate the culture. The study has indicated that under favorable environmental conditions the protoplasm of the progenitor of the culture possessed (at least) the potentiality to produce similar cells to the number represented by 2 raised to the 5071st power, or a volume of protoplasm greatly exceeding 10^{1000} times the volume of the Earth. I believe this result indicates beyond question that the protoplasm of a single cell may be self sufficient to reproduce itself indefinitely, under favorable conditions, without recourse to fertilization (4).

However, with this conclusion secure,

TABLE I

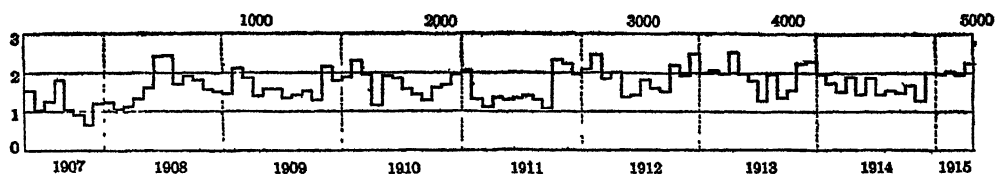
Record of the number of generations attained during each year of the life of the culture from May 1, 1907 to May 1, 1915

YEAR	GENERATIONS	DAILY AVERAGE DIVISION RATE
1	452	1.24
2	690	1.89
3	613	1.68
4	612	1.67
5	662	1.81
6	692	1.89
7	671	1.84
8	679	1.86
Average for 8 years.....	634	1.74

I was reluctant to discard the race and was tempted to keep it under control, but without such exacting daily observation

numbers, 11,700 generations attained by the culture during the 19 years of its life, to date since May 1, 1907. The vitality of the culture is further attested by the fact that it is continuously affording animals for various other experimental studies on *Paramecium* at Yale and elsewhere.

Careful studies of the rate of division of sub-lines derived from the main culture and bred under the most constant environmental conditions revealed the fact that there are inherent, *normal*, minor, periodic accelerations and depressions of the fission rate due to some unknown factor in cell phenomena. These were termed rhythms (5). In a search for the underlying factors of rhythms a complicated internal nuclear reorganization process was discovered and named endomixis (6). This process, in



GRAPH SHOWING THE RATE OF REPRODUCTION OF THE PEDIGREE RACE OF *Paramecium aurelia* DURING THE FIRST EIGHT YEARS OF CULTURE

The ordinates represent the average daily rate of division of the four lines of the culture, again averaged for each month. The vertical broken lines indicate the limits of the calendar years. The figures 1000, 2000, etc., represent generations and are placed above the periods in which they were attained.

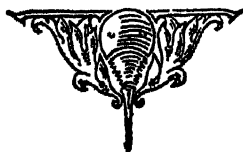
and recording of the daily division rate. Accordingly, it has been kept in this manner up to the present time (April, 1926). But from time to time thirty-day tests have been made of the vitality of the race under the former rigid culture conditions, and in each case the same general average division rate has been revealed as during the first eight years of its life. For example, during December, 1915, 52 generations; during December, 1917, 56 generations; during November, 1920, 54 generations, and during February, 1926, 53 generations were attained. On the basis of such tests it is fair to make the exceedingly conservative estimate of 600 generations attained each year since May 1,

essence, consists of a gradual disintegration and absorption of the macronucleus and the formation of a new one from the micronuclear apparatus. This results in the reorganization of the cell (endomixis) without the coöperation of two animals involving syncaryon formation (amphimixis) as in fertilization.

Endomixis obviously introduces an entirely new problem, though, of course, it in no way affects our former conclusion that fertilization, involving syncaryon formation, is not intrinsically a necessary phenomenon in the life history of the organism. Whether endomixis is a necessary factor for the continuance of the race is another question and is now being

LIST OF LITERATURE

- (1) CALKINS, G. N.: The Protozoa. 1901, pp. 60-61, 241.
- (2) JENNINGS, H. S.: Life and Death, Heredity and Evolution in Unicellular Organisms. 1920, p. 29.
- (3) WOODRUFF, L. L.: The life cycle of *Paramecium* when subjected to a varied environment. American Naturalist, vol. 42, 1908. Two thousand generations of *Paramecium*. Archiv f. Protistenkunde, Bd. 21, 1911.
- (4) WOODRUFF, L. L.: The problem of rejuvenescence in Protozoa, Biochemical Bulletin, vol. 4, 1915.
- (5) WOODRUFF, L. L., and BARTSELL, G. A.: Rhythms in the reproductive activity of Infusoria. Jour. Exper. Zool., vol. 11, 1911.
- (6) WOODRUFF, L. L., and ERDMANN, R.: A normal periodic reorganization process without cell fusion in *Paramecium*. Jour. Exper. Zool., vol. 17, 1914.
- (7) CALKINS, G. N.: Biology of the Protozoa. 1926, Chapter 10 *et seq.*
- WOODRUFF, L. L.: The physiological significance of conjugation and endomixis in the Infusoria. American Naturalist, vol. 59, 1925.
- These two publications contain extended discussions of the problem from different viewpoints.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

A NEW WORD FOR AN OLD THING

Being a review of *Behaviorism* by John B. Watson. New York (People's Institute Publishing Co.), 1925. 6 x 8 $\frac{5}{8}$; viii + 296. \$3.00.

By William Morton Wheeler, Harvard University

In this volume, advertised as "the first popular presentation of behaviorism," the author attempts to treat in a series of a dozen lectures, what he seems to regard as a new psychological dispensation which spurted from the intellects of a group of American investigators as recently as 1912. The presentation of scientific matter of such complexity and alleged novelty before a popular audience like that of the People's Institute is an undertaking before which an even more enthusiastic, virile and combative investigator than Watson might quail. And now the old-fashioned psychologists are in tears on account of the bull's behavior and the devastation he has wrought in their china-shop. Both parties are, of course, to blame—the china-shop keepers for setting such store by their fragile, antique wares and their love of exposing them with-

out adequate safeguards, and the bull for smashing them. Perhaps, however, the bull is the less culpable, because the shopkeepers have of late been too enthusiastically convincing him that he is a connoisseur in porcelain.

Psychology is universally admitted to be a queer science, and one can hardly fail to observe that its queerness, apart from the peculiarities inherent in its subjective subject matter, is due in no small measure to the mental peculiarities of its devotees. When we consider that, with very few exceptions, the men who have developed psychological science have been either philosophers, priests or pedagogues, or hybrids of all three, its strangely inhibited, not to say eunuchoidal, aspect is easily understood. To put the matter *crue, nue, verte et sans phrase*, these doctrinaire individuals seem always to have a horror of admitting to themselves and others that they are and will always remain individual mammals of the Family Hominidæ and the Order Primates. Their professions require that they shall give the impression that they subtly vegetate on cloud-banks of ratiocination and pure asexual love and that they possess little or no first hand acquaintance with the instincts, emotions

or appetites, not to mention uglier propensities. Moreover, these are the very castes to whom we consign the education of the young of our species, and the young must, of course, be carefully diverted from all curiosity in their abominable urges and longings. Hence the concentration on the most anæmic psychic processes—consciousness, sensation, perception, apperception, memory, attention, ideation, volition, etc., and the rationalizations, or “thobbing,” to use a term recently coined by Henshaw Ward, which compels the psychologist to slur over the real drives of human nature and to pursue his researches and writing, not as a scientist, but as a “*verkappster*” moralist. Pray, what would present day anatomy, physiology and medicine be like if the subject matter of these sciences had been handled by their teachers and investigators in a similar oldmaidish spirit?

After the older generation of psychologists had secreted many tons of literature as dry if not as dead as Tuthankamen's mummy, at the very time when a host of keenly observant novelists were writing the most illuminating studies of individual psychology, the youngsters broke away and are now frisking about in the less arid pastures of advertising and industrial psychology, intelligence testing, behaviorism, “*Gestalt*” and psychoanalysis. And the only excitement the oldsters can get up in self defence is to secrete more literature on such topics as the “Crisis of Psychology,” the soul and spiritualism (Driesch) or to admonish the youngsters to behave themselves in the interests of harmony (see the recent addresses of Madison Bentley and Miss Calkins). Of course Watson, as one of the most obstreperous of the youngsters, has been so frequently spanked that he has by this time undoubtedly developed ischial

callosities of some thickness. Since henceforth the application of the ferule in the same *locus* would be ineffectual, a more sensitive spot might be sought. To the biologist the whole situation is replete with fun and confusion.

The old definition of psychology as the science of conscious processes being too uninteresting, a new one was sought and found a few years ago by some of the mandarins, who defined it as the “science of behavior.” Naturally all the behaviorists at once jumped to the conclusion that they were psychologists. It is not clear, therefore, why Watson and his fellow behaviorists should be castigated for agreeing with the psychologists when they were straining themselves, like many modern theologians, to clothe their old science in more “peppy” habiliments. But Watson may be blamed for his failure to recognize and present behaviorism as a long-established, purely biological discipline. His lack of interest in the history of science has led him to regard himself as the Messiah of a new scientific dispensation dating from the year of grace 1912. Since it must be terribly humiliating to most biologists to feel that they have so long overlooked so promising a path to salvation, a brief historical exegesis may be introduced at this point.

This is Watson's definition of behaviorism:

“Behaviorism, is, then, a natural science that takes the whole field of human adjustments as its own. Its closest scientific companion is physiology. Indeed you may wonder, as we proceed, whether behaviorism can be differentiated from that science. It is different from physiology only in the grouping of its problems, not in fundamentals or in central viewpoint. Physiology is particularly interested in the functioning of parts of

the animal—for example, its digestive system, the circulatory system, the nervous system, the excretory system, the mechanics of neural and muscular response. Behaviorism, on the other hand, while it is intensely interested in all of the functioning of these parts, is intrinsically interested in what the whole animal will do from morning to night and from night to morning."

Now since man is an animal, his behavior must be animal behavior, and the department of biology which deals with this was certainly not inaugurated fourteen years ago. It may be of no particular interest to trace it to Aristotle, but we are justified in regarding Réaumur's work on insects, published during the first half of the eighteenth century, as at the same time the first popular presentation and the starting point of modern behaviorism. It was known at that time as "natural history" and its outlines were rather vague, but Isidore Geoffroy St. Hilaire in 1859 clearly outlined its scope under the name of "ethology," and Haeckel in 1866 and 1869 even more accurately defined it as "Relations-Physiologie der Thiere," though he called it "oecology." In 1888 Carl Semper designated it as the "Physiologie der Organismen" to distinguish it from the "Physiologie der Organe," and in 1894 Burdon Sanderson published the following lucid statement:

"Now the first thing that strikes us in beginning to think about the activities of an organism is that they are naturally distinguishable into two kinds, according as we consider the action of the whole organism in its relation to the external world or to other organisms, or the action of the parts or organs in their relation to each other. The distinction to which we are thus led between the *internal* and *external* relation of plants and animals has

of course always existed, but has only lately come into such prominence that it divides biologists more or less completely into two camps—on the one hand those who make it their aim to investigate the actions of the organism and its parts by the accepted methods of physics and chemistry, carrying the investigation as far as the conditions under which each process manifests itself will permit; on the other, those who interest themselves rather in considering the place which each organism occupies, and the part it plays in the economy of nature. It is apparent that the two lines of inquiry, although they equally relate to what the organism *does* rather than to what it *is*, and therefore both have equal right to be included in the one great science of life, or biology, yet lead in directions which are scarcely even parallel. So marked, indeed, is the distinction that Professor Haeckel some twenty years ago proposed to separate the study of organisms with reference to their place in nature under the designation of 'oecology,' defining it as comprising 'the relations of the animal to its organic as well as to its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes into direct contact.' Whether this term expresses it or not, the distinction is a fundamental one. Whether with the oecologist we regard the organism in relation to the world, or with the physiologist as a wonderful complex of vital energies, the two branches have this in common, that both studies fix their attention not on stuffed animals, butterflies in cases, or even microscopical sections of the animal or plant body—all of which relate to the framework of life—but on life itself."

E. Ray Lankester in 1889 also stressed the importance of ethology but called it

"bionomics," a term which has been little used. For many years the Germans have been employing "Biologie" *sensu stricto* for the same subject, while French zoologists, following the lead of Alfred Giard, retained St. Hilaire's designation. Emery and Waxweiler speak of it as "external physiology" and regard it as a preliminary or exploratory science destined eventually to be absorbed in physiology proper. That "behaviorism" is merely the most recent and most fashionable name for this long-established department of biology is sufficiently clear from the practical identity of Watson's and Burdon Sanderson's definitions. It may also be recalled, in connection with the first sentence of Watson's definition that John Stuart Mill in his *Logic* (1843) preceded St. Hilaire in the use of the term "ethology" for the science of human character, but since the character of an organism is revealed only in its reactions to its environment, that is by its behavior, there is no fundamental difference between animal and human ethology. Recently Bernard Hollander in his voluminous work "In Search of the Soul" calls attention to Mill's use of the term and adopts it for what is essentially human behavior.

It is evident, therefore, that there is nothing startlingly novel in the conceptions and methods employed by Watson and that both he and the psychologists seem to have been duped by a new word for an old thing. No doubt their deception is also due to the fact that the methods of ethological, or behavioristic science have proved to be so illuminating that, as Watson says (p. 17), "behavioristic formulations are becoming central in the whole field of what has hitherto been called 'the mental and moral sciences.'" In other words, ethological methods have been so rapidly and so aggressively in-

vading philosophy, ethics, sociology and religion that serious doubts have arisen among modern thinkers as to the usefulness of the concepts and methods which have been so long employed in those domains. *Hinc illa lacryma* on the part of the old doctrinaires.

If the foregoing considerations are kept in mind it is not difficult to evaluate Watson's work. In so far as it is physiology of the type known to biologists as ethology, or relational physiology, it is of the greatest interest and value, not only to them but also to the humanists, if we use that term to include all students of the Hominidæ—anthropologists, psychologists, sociologists and ethicists. His statements, however, on specifically psychological matters cannot be taken seriously. The obvious fallacies involved in the behaviorist's rejection of the data obtained by introspection in the domain of immediate experience have been set forth by a number of authors, and most recently by E. D. Martin, Driesch and Broad. As Driesch clearly states, "Even if the behaviorists were right in saying that the only class of conscious objects are sensations" [Watson would seem not to accept even these] "this very statement would itself be the result of 'introspection'! And further to what class of objects belongs the *truth* of the behavioristic theory itself, that there is nothing but sensations? Is this specific truth itself a sensation? The behaviorists would hardly dare assert that it is, I fancy. So we may say, in short, that the behaviorist *forgets himself* in his psychological theory. Behaviorism is a good method,—nay, the only method—in animal psychology; indeed in this part of psychology, all knowledge that is really 'psychological' can be acquired only indirectly, never directly, for the movements of the body are the only things

that are given immediately. But in what we may call the *first*, the original psychology, i.e. *my* psychology, conditions are, fortunately, different. And it is for this reason that all other psychologies, the psychology of the *other Ego* of animals, of instincts, etc., must go back to the first psychology as their very foundation. Not to use introspection in 'my' psychology would be to proceed as if I always made use of a mirror in order to see what I might see directly—or even worse!" And Broad goes so far as to class behavioristic views like Watson's among the "silly" theories, by which he means those that "may be held at the time when one is talking or writing professionally, but which only an inmate of a lunatic asylum would think of carrying into daily life. I should count Behaviourism, taken quite strictly, and certain forms of Idealism as 'silly' in this sense. No one in his senses can in practice regard himself or his friends or enemies simply as ingenious machines produced by other machines, or can regard his armchair or his poker as being literally societies of spirits or thoughts in the mind of God. It must not be supposed that the men who maintain these theories and believe that they believe them are 'silly' people. Only very acute and learned men could have thought of anything so odd or defended anything so preposterous against the continual protests of common sense "

Those who have come to regard living organisms as at the same time creative and remarkably conservative, historical beings will notice that Watson is little affected by such considerations and inclined to overstress the effects of environment and to underestimate the complexity of organized and inherited struc-

ture. He seems to regard all healthy infants as very much alike at birth and to account for their later differences as very largely due to the conditioning, reconditioning and unconditioning of their reflexes, to visceral and muscular habits, training, etc. The geneticists are dismissed (p. 78) with an amusing fiction about three hypothetical sons of John Smith, the economist, and the remark, "the geneticists are working under the banner of the old 'faculty' psychology. One need not give very much weight to any of their present conclusions." Similarly the psychoanalysts, many of whom have stressed the persisting ancestral tendencies of our species, are said to base their work "largely upon religion, introspective psychology, and voodooism," and this notwithstanding the fact that Watson has absorbed many of their teachings. They are also presented (p. 244) with a fictitious and amusing account of a psychopathic dog. Watson describes how he conditioned a normal dog till he became a most abjectly insane animal and how he then unconditioned and reconditioned him till he walked off with the blue ribbon at the dog show. All this is humorous but hardly fair to the psychoanalysts or admissible as a popular account of their views. The importance of environment and training may be underestimated by many biologists of the present time, but there is certainly a much greater "historical basis of reaction" in animals and man than Watson would have us believe. Yet notwithstanding all its faults, the volume will be found to contain a great amount of valuable matter, especially on infant behavior, and many fresh incentives to the further investigation of man's basic nature.

BRIEF NOTICES

EVOLUTION

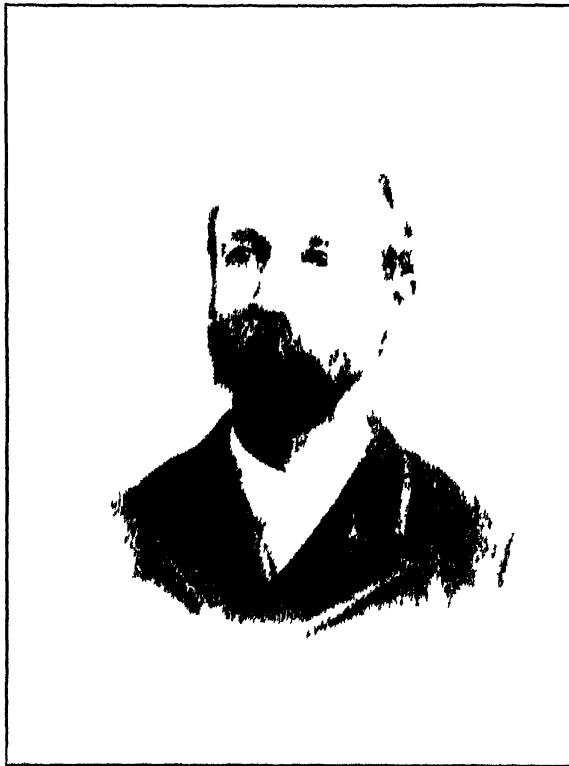
EVOLUTION EXAMINED IN THE
LIGHT OF REVELATION AND
REASON

By Albert P. Schack Frederick H. Hitchcock
\$2.50 6½ x 8½, 121 New York

Physiognomy is not yet an exact science. Nevertheless, as Galton recog-

Fundamentalists. The parties to any controversy ought, at least, to know what their opponents look like. To this end we propose to publish in THE QUARTERLY REVIEW OF BIOLOGY, as opportunity and occasion may offer, a *Fundamentalist Portrait Gallery*.

It is with great satisfaction that we open this exhibition with the portrait of



ALBERT P. SCHACK

nized when he began his work on composite photography, everyone is considerably influenced in his judgments regarding the practical conduct of life, by physiognomic considerations. Experience demonstrates that, on the whole, these judgments are far more often right than wrong.

the eminent divine and author, Albert P. Schack.

Evolution Examined in the Light of Revelation and Reason is a book that all biologists should read. Its provenience is set forth as follows by the author (p. 6): "A few years ago, the lack of a work, and the demand for one, by some author

fold the subject, and make it plain to the people, and at the same time withstand the scrutiny and criticism of all the scientists, kept pressing upon me, so that I finally decided, having been thus suitably prepared by education, as well as by a careful study of the specific subject in all its aspects, that I might properly undertake the work for the sake of humanity, and for the honor of God and the Divine Truth."

Mr. Schack holds that "all kinds of life, or specific principles, are *inserted*, and are not evolved or developed merely out of and by the forms themselves," though he admits that this is often the appearance of things. "As an example or illustration of life entering and animating suitable forms, I have put a hair from a horse's tail in a vessel of water for some days, and have seen one end of it swell into a head, distinctly visible under a magnifying glass; and life flowing into it, which may be supposed to be everywhere imminent or outpressing from within, it became a snake or eel swimming in the water, because it was such a suitable sheath or form that such corresponding primitive life could inhabit and use it. This simple experiment can be tried by anyone, and the result will be seen to be as above stated" (p. 15).

The reviewer finds it difficult to refrain from quoting extensively from this informing volume, but considerations of space are imperative. We must content ourselves, therefore, with one more extract, which constitutes the whole of Chapter XI. It is not only interesting in content, but is also something of a literary feat. Few books can boast of a chapter which consists of only one sentence!

WARNING TO STUDENTS

"Hence I would warn those who are tempted to be seduced by the seemingly

plausible hypotheses of the really blind materialists, to hold fast to the Word of God, not allowing the few portions of it which seem objectionable or difficult to understand, to prevent them from receiving it as a whole, or the vastly larger portion, which should not be objectionable to any, and of which we can get some understanding, if we study it, and humbly ask the Lord to help and enlighten us; recollecting that the whole Word is primarily and in some parts solely parabolic or symbolic of spiritual or internal things—motives—goodness and truth against evil and falsity, and in general of matters relating to God and the human soul" (pp. 102 and 103).

This book is priceless, in the technical Britannic sense of that word.

INDIAN BIRD LIFE. *Or the Struggle for Existence of Birds in India.*

By Douglas Dewar

John Lane, the Bodley Head

7s. 6d. 5½ x 7½; xv + 276 London

This is an important, original contribution to the literature of organic evolution. It deals with the problem of checks to the avian population in India, on the basis of specific field observations rather than upon pseudo-philosophic platitudes, which all too frequently appear in lieu of evidence in the literature of evolution. Coupling extensive personal observations in the field with a remarkably thorough combing of the detailed ornithological literature, the author attempts to determine into which of the following categories the checks to avian population growth actually fall:

"1. Those of which the operation is entirely indiscriminate or haphazard; such operate equally on the fit and unfit, the weak and the strong, birds of gay plumage and birds of sombre hue.

"2. Those of which the operation is largely indiscriminate or haphazard.

"3. Those which operate only on the unfit, the weak, or birds ill-adapted to their environment.

"4. Those which operate mainly on the unfit, the weak, or birds ill-adapted to their environment" (p. 258).

The conclusions reached are as follows: "From the facts that the greatest destruction is to eggs and young birds and that the forces which destroy adult birds for the most part act indiscriminately as opposed to selectively, the inference must be drawn that, speaking generally, the individuals which survive longest in the struggle for existence are the lucky ones, rather than the most fit. It is, of course, true that other things being equal, the individuals which are fittest or strongest or best suited to their environment will have the best chance of survival. As a matter of fact other things are rarely equal. The existence of a bird may perhaps not inaptly be compared to a game of cards in which the element of chance is a very important factor. Although it is agreed that *A* is the most skilled of the players taking part in the game, no one, before any particular game, would give long odds on *A* winning, because far more depends on the hands dealt than on the skill of the players. So is it with birds. If we mark down, let us say, four individuals of a species, each living in an area at a distance from the others, it would not be prudent to give odds that the strongest of the four individuals will outlive the other three. The struggle for existence of birds results in the weeding out of the unlucky rather than the less fit.

"In view of the evidence before us it seems difficult to accept the view held by some that all the physical and anatomical features of every species are the

result of a process whereby only the fit survive to produce young, which tend to inherit the fitness of the parents. Rather are those characteristics the result of the innate tendency of the majority of individuals of a species to vary in certain definite directions. Natural selection, the survival of the fittest, seems normally to come into action where variations markedly unfavourable to the individual appear.

"Natural selection, then, seems to have played only a very subordinate part in the production of the colouring and the anatomical and physical features of the various species of birds. This, however, does not mean that it has not played its part in evolution. There are conditions in which the force comes actively into play. Natural selection, for instance, has probably helped to determine such features as the number of eggs which compose the normal clutch for each species, the number of clutches laid in the year, the time of nesting, the situation of the nest, the times of migration and the degree of pugnacity possessed by the average individual of any species" (pp. 260-261).

The book is of interest and value to the student of the biological aspects of the population problem, as well as to the evolutionist. Unfortunately it is not adequately indexed, but after all this is only a minor defect in a really significant contribution.



LIFE, MIND, AND SPIRIT. (*Being the Second Course of The Gifford Lectures Delivered in the University of St. Andrews in the Year 1923 under the General Title of Emergent Evolution.*)

By C. Lloyd Morgan Henry Holt and Co.
\$3.75 5 $\frac{1}{8}$ x 9; xix + 316 New York

This book attempts to formulate a

philosophical interpretation of the order of nature—the evident teleological structure and behavior of the universe. The solution offered is frankly theistic. Essentially the order of nature is Divine Purpose objectively expressed, and there the case rests. This manner of disposing of the problem is neither particularly novel, nor, as the whole history of philosophic thought shows, especially helpful. At the same time it must be said that the author puts the case in an extremely persuasive way, much better calculated to seduce the modern scientific reader than, for example, were the writings on natural theology of the eighteenth and early nineteenth centuries. Biologists will do well to read this book.



THE RELATION BETWEEN SCIENCE AND THEOLOGY. (*How to Think About It.*)

By C. Stuart Gager

The Open Court Publishing Co.

\$1.00 5 x 8; 87 Chicago

This little tract of the times is written in a spirit of deep reverence—both to God and to science. Its philosophy is summed up in the following statement: "What has evolution to do with religion? In a sense, nothing. Science has to do with so-called secondary causes; religion has to do with man's relation to the Great First Cause—Myself and God" (p. 79). As a bit of conciliatory exegesis it is well done.



THE PASSING OF THE PHANTOMS. *A Study of Evolutionary Psychology and Morals.*

By C. J. Patten

Kegan Paul, Trench, Trubner and Co.

2s. 6d. 4½ x 6½; 95 London

The author seems to be more sympathetic than coldly analytic in his ex-

periences with family pets, especially a hawk. He attributes a somewhat higher psychic life to lower animals than perhaps most students of animal behavior are disposed to do. On this not wholly indubitable base he builds up a theory of the evolution of man's mental and moral powers. The book is more entertaining than convincing.



THE STRATIGRAPHY AND FAUNA OF THE HACKBERRY STAGE OF THE UPPER DEVONIAN. (*Contributions from the Museum of Geology, University of Michigan. I.*)

By Carroll L. Fenton and Mildred A. Fenton
The Macmillan Co.

\$2.75 6¼ x 9½; xi + 260 New York

Describes, with abundant illustrations on 45 plates, the fossils found in the uppermost member of the Devonian section (the rocks of the Hackberry stage) in North Central Iowa.



GENETICS

HEREDITY

By A. Franklin Shull *McGraw-Hill Book Co.*

\$3.00 6¼ x 9½; xi + 287 New York

An excellent introductory text to the field of modern genetics. Developed in connection with a lecture course to large classes of college students without preliminary biological training, the book has solved well the difficult pedagogical problem of presenting an intricate subject in a clear, attractive, and at the same time thoroughly sound, manner. Those giving beginning courses in genetics in colleges and universities will do well to consider it carefully for use as a text. Furthermore it is, on the whole, the best book that has come to our attention for the intelligent layman who wishes to get

a sound understanding of the fundamental principles of heredity. The last eight chapters are devoted to various aspects of human genetics. A glossary of technical terms and an adequate index complete the volume.



PRAKTISCHE ÜBUNGEN ZUR VERERBUNGSLEHRE FÜR STUDIERENDE, ÄRZTE UND LEHRER. (*In Anlehnung an den Lehrplan des Erbkundlichen Seminars von Prof. Dr. Heinrich Poll*). (*Biologische Studienbücher. Band I.*)

By Dr. Günther Just Theodor Fisher
Rm. 3.50 Freiburg im Breisgau

6½ x 9½; 88 (paper)

This is an outline of a course of eighteen laboratory exercises in genetics as used by the author and Professor Poll in an elementary course at Berlin. The first six exercises deal with the biometric analysis of variation; the next seven with the analysis of Mendelian experiments; and the last five with human pedigrees. It is a well planned elementary course.



THE THEORY OF THE GENE.

By Thomas Hunt Morgan

Yale University Press.

\$4.00 6½ x 9½; xvi + 343 New Haven

This book will be the subject of an extended review by Professor Julian Huxley, in the next number of THE QUARTERLY REVIEW OF BIOLOGY.



GENERAL BIOLOGY

NATURALIST'S GUIDE TO THE AMERICAS. *Prepared by the Committee on the Preservation of Natural Conditions of The Ecological Society of America, with assistance from numerous organizations and*

individuals. Assembled and edited by the Chairman, Victor E. Shelford.

The Williams & Wilkins Co.

\$10.00 6½ x 9½; xv + 761 Baltimore

This comprehensive treatise, produced by the coöperative efforts of The Ecological Society of America, discusses in detail the natural habitat for living things in North America, Central America, and the northern part of South America, together with certain of the islands in the Atlantic and Pacific Oceans. The first three parts of the book are devoted to the uses, values, and management of natural areas and the original biota of the Americas north of the Amazon. The fourth part, which takes up the bulk of the book, is devoted to detailed descriptions of natural areas and regions within named political subdivisions. The primary object of the book is stated to be "To locate natural areas so as to make them available to naturalists." For each territory the account describes: (1) the region as it was before being modified by civilization; (2) the general physiographic features, and (3) general and local plant and animal communities. The original conditions of the biota are then contrasted with the present modified condition. The book is a valuable contribution to the literature of general natural history.



ERGEBNISSE DER BIOLOGIE.

Edited by K. v. Frisch, R. Goldschmidt, W. Rubland and H. Winterstein.

Julius Springer

36 reichsmark

Berlin

6½ x 9½; viii + 670 (paper)

The QUARTERLY REVIEW OF BIOLOGY extends a hearty welcome to this new periodical which in some sense covers the same field. It is announced that the *Ergebnisse der Biologie* will treat general

physiology (as distinguished from physiology primarily of medical interest) in much the same way that the *Ergebnisse der Anatomie und Entwicklungsgeschichte* and the *Ergebnisse der Physiologie* deal with their respective fields. This first number opens with a paper of 323 pages by E. Biedermann on the comparative physiology of the integument of vertebrates. The second paper is by F. Bachmann on the ascent of sap in plants. The third is by Hugo Kaho on the relation of the plant cell to salts. The fourth paper, by D. N. Prianischnikow, deals with ammonia, nitrates and nitrites as nitrogen sources for higher plants. The two final papers discuss respectively the social psychology of birds (by David Katz), and bird migration (by Horst Wachs). There are detailed indices and literature lists.



LA CINÉTIQUE DU DÉVELOPPEMENT. *Multiplikation cellulaire et Croissance.*

By E. Fauré-Fremiet (Preface by M. L. F. Hennequy)

Les Presses Universitaires de France
30 francs 6 $\frac{1}{2}$ x 9 $\frac{1}{2}$; viii + 335 Paris

This is an important and valuable addition to the literature of general biology. It reviews the existing knowledge and opinion about the physics and chemistry of growth and development in a thorough manner. The material is discussed under the following heads: The cellular system from a static point of view; cellular growth; the changes of state in the cellular system in the course of division; the transformations of energy in the course of embryonic development; the laws of growth of the body and of the organs; the multiplication of free cells—Protozoa; the multiplication of cells *in vitro*—tissue cultures. There are extensive bibliographies, but unfortunately an index is lacking.

COMPARATIVE PHYSIOLOGY

By Lancelot T. Hogben The Macmillan Co.
\$3.00 5 $\frac{3}{4}$ x 8 $\frac{1}{2}$; xiv + 219 New York

This book aims to give in brief space an account of the physiology of the lower organisms, primarily for the purpose of stimulating students of zoölogy to further research in this field. It is thoroughly modern in its viewpoint, emphasizing the physico-chemical approach to the problems of physiology. The topics treated are as follows: muscular contraction; ciliary activity, amoeboid motion and color response; secretion; respiration; nutrition; the circulation of body fluids; endocrine co-ordination; the mechanism of nervous conduction and excitation; the analysis of behavior in animals; the fertilization of the egg; inheritance; physiology of development.



PAPERS FROM THE DEPARTMENT OF MARINE BIOLOGY OF THE CARNEGIE INSTITUTION OF WASHINGTON. Vol. XXIII (Publication No. 344).

Some Marine Bottom Samples from Pago Pago Harbor, Samoa, by M. N. Bramlette. *Proportions of Detrital Organic Calcareous Constituents and their Chemical Alteration in a Reef Sand from the Bahamas*, by Marcus I. Goldman. *Report on a Bacteriological Examination of "Chalky Mud" and Sea-Water from the Bahama Banks*, by N. R. Smith. *Recent Foraminifera from Porto Rico*, by J. A. Cushman. *Fossils from Quarries near Suva, Viti Levu, Fiji Islands, and from Vavao, Tonga Islands, with Annotated Bibliography of the Geology of the Fiji Islands*, by Wendell C. Mansfield. *Miocene Corals from Trinidad*, by T. W. Vaughan and J. E. Hoffmeister.

Carnegie Institution of Washington
\$2.50 Washington, D. C.

6 $\frac{1}{4}$ x 10; 134 + 7 plates (paper).

The contents of this volume seem

likely to be of greater interest to the oceanographer and the paleontologist than to the general biologist.



PRACTICAL PHOTO-MICROGRAPHY.

By J. E. Barnard and Frank V. Welch

Longmans, Green and Co.

\$6.00 5 $\frac{3}{4}$ x 8 $\frac{1}{2}$; xii + 316 New York

A second edition, issued after a lapse of fourteen years since the appearance of the first, of the standard work in English on photo-micrography. The senior author, who has lately been much in the public eye in connection with his collaboration with Gye on the cancer problem at the Medical Research Council's laboratory in London, is one of the foremost authorities in the field. In the second edition attention has been primarily given to a fuller description of methods rather than apparatus, because the authors find no outstanding advance, either on the optical or mechanical side, in the past fourteen years. The book constitutes a standard reference source for all those who use photo-micrography in their work.



HUMAN BIOLOGY

THE NORTHERN TRIBES OF NIGERIA. (*An Ethnographical Account of the Northern Provinces of Nigeria Together with a Report on the 1921 Decennial Census.*)

By C. K. Meek Oxford University Press

36s. 6 x 9; Vol. I, xviii + 312 London

Vol. II, viii + 277

This work is an important contribution to anthropology. The material is logically arranged, presented with great clearness and some degree of literary charm, and considers data of interest and value to the student of almost any aspect of human biology. There is first given a general description of the country

itself, considered as a habitat for human beings. This is followed by an historical section, with a good deal of interesting archaeological material. Then the various aspects of the native culture are considered in detail, beginning with the economic life. The political aspect of the cultural life is first discussed in relation to social organization, and then in regard to the system of government and law. The mental and spiritual life as revealed in language, law, and religion, receives thorough treatment. Part II of the second volume is of especial interest to students of the population problem, since it deals in detail with the census of the provinces of Northern Nigeria taken in 1921.



AUSTRALIAN TOTEMISM. (*A Psycho-analytic Study in Anthropology.*)

Géza Róheim (with an introduction by M. D. Eder) George Allen and Unwin, Ltd.

35s. 6 $\frac{1}{2}$ x 10; 487 London

Doctor Róheim attempts to explain the origin of the most primitive form of culture, totemism, on the theory that it is the result of a primeval crime, in which the sons of a Cyclopean family killed their tyrannical father, ate his body, and then married the females left about. Ever since then the sons, and their descendants, have been torn between the two emotions of repentant remorse over killing the old man, and triumphant joy at having got the ladies. As a result of these mixed emotions the taboos of incest and of eating the animal have grown up, as well as the ritual of totemic sacrament and organization into totem clans. It seems doubtful that this queer theory, reached by the psychoanalytic route, will be accepted by anthropologists. However, the author is a man of standing and marshals a large array of evidence with great ingenuity. On these accounts

the book cannot be lightly swept aside. It will interest the psychologist as well as the anthropologist. There is an extensive bibliography and index.



THE PEDIGREE OF THE HUMAN RACE.

By *Harris H. Wilder Henry Holt and Co.*
\$3.25 6 x 9; xiv + 368 New York

A sound treatise on the natural history of the primates has long been needed. This need is admirably met in the present book. One reads it with a feeling of confidence and security, because of the author's critical judgment in zoological matters. The book is divided into six chapters, of which the first reviews existing knowledge regarding the groups of primates now living. Chapter II deals with extinct forms related to man, reviewing the history of mammalian evolution. Chapter III treats of fossil men. Chapter IV, besides tracing the pedigree discusses the nature of the evidence and modes of reasoning by which present conclusions as to the evolution of man have been reached. Chapter V describes the differential characteristics of living races of men. The final chapter discusses the classification of human races. The book is well illustrated and indexed.

INTERNATIONAL ASPECTS OF BIRTH CONTROL. (*The Sixth International Neo-Malthusian and Birth Control Conference, Vol. I.*)

PROBLEMS OF OVERPOPULATION. Vol. II.

Edited by *Margaret Sanger*

American Birth Control League, Inc.
\$2.00 5½ x 8½; xii + 244 (paper) New York
\$2.00 5½ x 8½; 208 (paper)

These two volumes contain the official

report of the proceedings of the International Birth Control Conference held in New York in March, 1925. The first volume is devoted to reports on the present status of the birth control movement in different countries and states of this country, together with congratulatory and uplifting messages from various prominent persons. The second volume is devoted to the more scientific papers which were read. Students of the population problem may find these volumes useful for reference, although they contain little that is original. Unfortunately there is no index.



THE MEDICAL DEPARTMENT OF THE UNITED STATES ARMY IN THE WORLD WAR. VOLUME XV. STATISTICS. Part 2. *Medical and Casualty Statistics (Based on the Medical Records of the United States Army April 1, 1917, to December 31, 1919, inclusive).*

By *Maj. Albert G. Love*

Government Printing Office
\$3.00 Washington, D. C.

7½ x 10; xiv + 1368

A potentially profitable source book for the student of human biology.



ZOOLOGY

THE BIOLOGY OF THE PROTOZOA.
By *Gary N. Calkins Lea and Febiger*

\$7.50 6½ x 9½; ix + 623 Philadelphia

This is a masterpiece of textbook writing and is certain to become a classic in the field which it so thoroughly covers. The plan and scope of the book are sufficiently indicated by the chapter headings which are as follows: Introduction; Nuclei and kinetic elements; Structural differentiations; General physiology; Reproduc-

tion; Special morphology and taxonomy of the Mastigophora; Special morphology and taxonomy of the Sarcodina; Special morphology and taxonomy of the Infusoria; Special morphology and taxonomy of the Sporozoa; Vitality; Phenomena accompanying fertilization; Effects of reorganization and the origin of variations in the Protozoa. An enormous amount of careful painstaking, critical work must have gone into the preparation of the taxonomic portions of the treatise, and they will be correspondingly useful to all students of protozoology. Throughout the book the author stoutly maintains his well known position regarding the theoretical significance of the life cycle of Protozoa, a position with which many other biologists are not in entire agreement.



BIOLOGIE DER SCHMETTERLINGE. (*Biologische Studienbücher. III.*)

By Dr. Martin Hering Julius Springer
Rm. 18 6½ x 9½; vi + 480 (paper) Berlin

The introduction to this detailed treatise on the biology of butterflies deals first with their general anatomy, then with their phylogeny and taxonomic relationships. This introductory portion is followed by three main sections which take up the bulk of the book. The first of these deals with the ontogenetic development up to the imago; the second with the life of the imago; and the third with general problems, such as geographic distribution, alternation of generations, polymorphism, enemies of butterflies, experimental biology, etc. There is a brief bibliography of general works, and adequate indices. Altogether this is a welcome addition to zoological literature, in a direction to which textbook writing seems to be definitely turning—the preparation of more adequate

treatises on special groups than can possibly be included in general textbooks.



A WILD-ANIMAL ROUND-UP. (*Stories and Pictures from the Passing Show.*)

By William T. Hornaday

Charles Scribner's Sons

\$5.00 6½ x 9; xii + 372 New York

This contribution to the literature of popular natural history by the Director of the New York Zoological Gardens is largely made up of previously printed magazine articles, going back in some cases to 1908. It falls into three main parts, the first dealing chiefly with big game hunting adventures, mostly in the early days in our own western country. Part II discusses mainly the disappearance of big game animals in various parts of the world. The final portion of the book is devoted to the modern development of taxidermy. Every lover of nature will find it an entertaining volume, though its science is perhaps sometimes a little rough and ready, and its manner occasionally transgresses the canons of good taste. It is well indexed and most interestingly illustrated.



THE NEMATODE PARASITES OF VERTEBRATES.

By Warrington Yorke and P. A. Maplestone,
with Foreword by C. W. Stiles

P. Blakiston's Son and Co.

\$9.00 6½ x 10; xi + 536 Philadelphia

This is a thorough and detailed treatise on the taxonomy of the nematode worms living parasitically in vertebrate animals. It is extensively illustrated with line drawings, and contains adequate keys for the identification of the genera and a bibliography of 684 titles. In the Foreword there is an open letter ad-

dressed to "unborn helminthologists." It makes an impassioned and touching appeal that they do their taxonomic duty by worms, when their time comes. This letter adds just that serious touch needed to avert whatever slight possibility there might otherwise have been that this book as a whole would be taken in a spirit of levity. For who could contemplate the idea of an "unborn helminthologist" lightly?



ZOOLOGIE IM GRUNDRISSE.

By *Walter Stenpell* Gebrüder Borntraeger
6,90 marks *Berlin*

Lieferung 3, 7½ x 10½; 178 (paper)

6,60

Lieferung 4, 7½ x 10½; 176 (paper)

The third *Lieferung* of this general textbook of zoology already noticed in Number 2 of *THE QUARTERLY REVIEW* completes the first section dealing with morphology and taxonomy, and makes a beginning on the second main division of the work, which treats of physiology and development. This physiological section starts with a discussion of the composition of the body, followed by an account of the metabolism of material. This is followed, in the fourth instalment, by a discussion of the metabolism of energy, which includes a long section on the reactions of animals to stimuli. The account of reproduction and embryonic development is begun.



A NATURALIST IN EAST AFRICA. *Being notes made in Uganda, ex-German and Portugese East Africa.*

By *G. D. Hale Carpenter*.

Oxford University Press

15 shillings 6 x 9; 187 + 8 plates *London*

Dr. Hale Carpenter, well known for

his interesting book of a few years ago, "A Naturalist on Lake Victoria," again publishes a series of extracts from his notebooks of observations collected during his wanderings as an officer of the Uganda Medical Service. The result is a valuable contribution to natural history, especially in regard to the problems of variation and mimicry in butterflies. Perhaps the most important part of the book is a detailed account of extensive experiments on the relative edibility of insects. It is well illustrated and indexed.



ANIMAL LIFE IN THE SEA.

By *R. J. Daniel* Hodder and Stoughton, Ltd.
5s. 6d. 5¼ x 8¼; 119 *London*

This little book, written in a simple and lucid style, evidently intended for lay readers, is a fine example of popular science at its best. The contents are as follows: Life in the shallow seas; The deep sea; Some large fish of the sea; The giant squid; Some whales; Some extinct marine monsters; The great sea serpent. It is entertainingly and significantly illustrated. We commend it to our readers, and congratulate the author on so fine an achievement.



THE SECRETS OF THE EAGLE AND OF OTHER RARE BIRDS.

By *H. A. Gilbert and Arthur Brook*

Arrowsmith

10 shillings 6¼ x 8¼; 196 *London*

The superb photographs of birds reproduced in this volume make it worthy the serious attention of zoologists. Nearly half the book is devoted to the golden eagle, its nest and nestlings. Some of the other birds discussed and photographed are not particularly rare, but the

photographs of them are highly unusual in quality. Every student of birds, whether professional or amateur, will find delight in this book.



L'ÉVOLUTION DE L'ORNITHOLOGIE.

By Maurice Boubier Félix Alcan

10 francs $4\frac{3}{4} \times 7\frac{1}{2}$; 308 (paper) Paris

There is a real need for brief but comprehensive and accurate histories of the various sub-divisions of the biological sciences. An excellent contribution in this direction for ornithology is made by Doctor Boubier in this volume. It recounts in a pleasant and easy style the development of knowledge about the various aspects of ornithology. It should be in every general biological library.



TAXIDERMY AND MUSEUM EXHIBITION.

By John Rowley. (Preface by Frank M. Chapman.) D. Appleton and Co.

\$7.50 $6\frac{1}{2} \times 9\frac{1}{2}$; xvi + 331 New York

In this comprehensive didactic treatise America's foremost taxidermist details the secrets of his craft. As in any other art, it is probable that in taxidermy genius cannot be transferred by teaching, but so far as technical equipment is concerned, this book covers the ground thoroughly. It will be the standard work on the subject for a long time to come. It is fully illustrated and indexed.



PORTRAITS IN THE LONDON ZOO.

By Silvia Baker G. P. Putnam's Sons

15 shillings $7\frac{3}{4} \times 10\frac{1}{4}$; 111 London

This delightful book will charm every lover of animals. The text is insignificant in amount and unimportant in content, but the tinted line drawings are

superb. With an economy of line which suggests Rouveyre, the artist has imbued her figures of all sorts of animals with real life and character.



A KEY TO THE SNAKES OF THE UNITED STATES, CANADA, AND LOWER CALIFORNIA.

(Michigan Academy of Science, Arts and Letters. Vol. IV. Part II.)

By Frank N. Blanchard The Macmillan Co.

\$1.75 $6\frac{1}{4} \times 9\frac{1}{2}$; xiii + 65 New York

This useful key lists 191 species and subspecies of North American snakes, exclusive of continental Mexico and Central America. The characters used for identification do not involve any necessity for dissection or for examination of teeth. Data are given on the geographic distribution of each species and subspecies.



PAPERS FROM THE DEPARTMENT OF MARINE BIOLOGY OF THE CARNEGIE INSTITUTION OF WASHINGTON. Vol. XXIV (Publication No. 345).

Taxonomy of the Amebas with Descriptions of Thirty-nine New Marine and Fresh-water Species.

By Asa Arthur Schaeffer

Carnegie Institution of Washington

\$4.75 Washington, D. C.

$9\frac{1}{4} \times 11\frac{1}{2}$; 116 + 12 plates (paper)

In this beautifully illustrated monograph the author describes 39 new species and 11 new genera of amebas, and proposes a system of classification for the group based upon general morphology. In connection with the descriptions of the species numerous interesting observations on behavior and physiology are included.

REPORT ON A COLLECTION OF SEA TROUT SCALES FROM THE RIVER HOPE AND LOCH HOPE IN SUTHERLAND. (*Fishery Board for Scotland. Salmon Fisheries. No. 1.*)

By G. Herbert Nall H. M. Stationery Office
3 shillings 6½ x 9½; 22 (paper) Edinburgh

Original data of interest to anyone working on the problems of growth or senescence.



BOTANY

THE SCENT OF FLOWERS AND LEAVES. *Its Purpose and Relation to Man.*

By F. A. Hampton Dulau and Co., Ltd.
6 shillings 5½ x 7½; vii + 135 London

This is an extremely interesting and entertaining little book about a neglected aspect of botany. It is simply and pleasantly written, but contains a wealth of unusual information. The topics treated are as follows: The sense of smell; Composition of the scent; Origin and development of the scent; Distribution of the essential oil in the plant; Function of scent; Insects and the scent of flowers; Scent in relation with botanical character; Classification; Our appreciation of scent; Scent in the garden; Extraction of scent and the manufacture of perfume; History. The book is adequately indexed.

THE FAMILIES OF FLOWERING PLANTS. I. DICOTYLEDONS. *Arranged According to a New System Based on Their Probable Phylogeny.*

By J. Hutchinson Macmillan and Co.
\$6.00 6 x 9; xiv + 328 London

The principles on which this new systematic arrangement of the families of flowering plants are based are these:

Plants with sepals and petals, associated with other floral and anatomical characters also primitive, are regarded as more ancient phylogenetically than plants without sepals or petals. This is based on the theory that the parts of an angiospermous flower are modified leaves. Free parts are regarded as primitive, and connate or adnate parts as more recent. The spiral arrangement of parts is regarded as more primitive than the cyclic, and numerous free stamens as earlier than the few or connate. Also the hermaphrodite flower is regarded as preceding the unisexual flower. Resemblances are emphasized rather than differences. The book is well illustrated and indexed.



PHYSIOLOGICAL FEATURES OF ROOTS, WITH ESPECIAL REFERENCE TO THE RELATION OF ROOTS TO AERATION OF THE SOIL. (*With a Chapter on Differences Between Nitrogen and Helium as Inert Gases in Anaerobic Experiments on Plants, By Edward E. Fries.*)

By William Austin Cannon

Carnegie Institution of Washington
\$1.25 Washington, D. C.

7 x 10; iii + 168 (paper)

With great elaboration of detail this book reports the results of a critical experimental study of the relation of root growth to soil aeration in a wide range of plants. The two main topics dealt with in the research are: First, the effect on root growth of concentrations of carbon dioxide in the soil; and, second, the influence of oxygen supply. An interesting point of general biological significance is the emphasis laid upon the individuality of the plant as a factor in the physiological results obtained. This factor is too often neglected by both plant and animal physiologists.

BIOLOGIE DER BLÜTENPFLANZEN. (Eine Einführung an der Hand mikroskopischer Übungen.) (Biologische Studienbücher. Band II.)

By Prof. Dr. Walther Schoenichen

Theodor Fischer

Rm. 6.60

Freiburg im Breisgau

6½ x 9½; 216 (paper)

The topics dealt with in this brief practical introduction to plant biology are: The biology of the root; the biology of the stem; the biology of leaves; the biology of the flower; the distribution of seeds and roots. It is fully and significantly illustrated with 307 line cuts, all semidiagrammatic in character, but in the clearest possible way bringing out the principles which they are intended to illustrate. It should be translated into English.



PLANT DISEASE FUNGI.

By F. L. Stevens The Macmillan Co.

\$5.00 5½ x 8½; vi + 469 New York

This is a thorough, systematic treatise on the taxonomy and morphology of fungi pathogenic to plants. The book is well illustrated and has determinative keys to the genera. Descriptions of diseased hosts are omitted.



MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY.

Vol. XVII, Nos. 85 to 89. (Publication No. 362.) No. 85. *Development of the Human Embryo During the Period of Somite Formation, Including Embryos with 2 to 16 Pairs of Somites*, by George W. Bartelmez and H. M. Evans. No. 86. *Origin and Development of the Rete Ovarii and the Rete Testis in the Human Embryo*, by Karl M.

Wilson. No. 87. *Physiological Study of Cortical Motor Areas in Young Kittens and in Adult Cats*, by Lewis W. Wied and Orthello R. Langworthy. No. 88. *Lymphatics and Blood-Vessels of the Ovary of the Sow*, by Dorothy H. Andersen. No. 89. *Relation of Onset of Decerebrate Rigidity to the Time of Myelination of Tracts in the Brain-Stem and Spinal Cord of Young Animals*, by Orthello R. Langworthy.

Carnegie Institution of Washington

\$3.25

Washington, D. C.

9½ x 11½; 3 + 140 (paper)

This volume of contributions from the Carnegie Laboratory of Embryology well maintains the high standard which the biological public has learned to expect from this laboratory. The first paper in the volume is perhaps the one of greatest technical importance, while the last probably has the greatest general biological interest. It indicates a definite correlation between the time of myelination of the central nervous system and the appearance of decerebrate rigidity.



L'ANATOMIE EN POCHE.

By Victor Pauchet and S. Dupret

Gaston Doin et Cie

25 francs 4½ x 7; 316 (paper) Paris

Each page of this little pocket anatomy contains a clear, somewhat schematic diagram of the structure of a small portion of the human body. Every feature shown on the diagram is then carefully labeled. The result is excellent. Almost at a glance the memory on a detailed anatomical point can be refreshed or re-established. There are in all 297 of the little plates, and together they cover all the essential features of gross human anatomy. The book ought to be a boon to medical students, and to beginning surgeons.

THE HISTOLOGY OF THE MORE IMPORTANT HUMAN ENDOCRINE ORGANS AT VARIOUS AGES.

By *Eugenia R. A. Cooper*

Oxford University Press

\$4.00 xiii + 119 New York

This is a useful piece of morphological work for investigators dealing with any phase of the endocrine problem. Detailed accounts are given of the normal histology, and the changes with age, of the pituitary, the suprarenal, the thyroid, the parathyroid and the thymus glands. It is well illustrated, chiefly with microphotographs. There is a bibliography of 112 titles, and detailed author and subject indices.



DIE PATHOLOGISCH-HISTOLOGISCH-EN UNTERSUCHUNGSMETHODEN.

By *Prof. Dr. G. Schmoll. F. C. W. Vogel*
20 marks $6\frac{1}{2} \times 9\frac{1}{2}$; x + 481 (paper) *Leipzig*

The fourteenth edition of this standard *vide-mecum* of histological methods in the field of pathology, differs chiefly from the last preceding edition in the fact that the chapters on embedding and frozen section technique have been rewritten. Zoological laboratories will find this a useful reference work.



ELEMENTS OF SURFACE ANATOMY. (For Students of Medicine.)

By *I. MacLaren Thompson*

E. and S. Livingstone

5s. $5\frac{1}{4} \times 7\frac{1}{2}$; 172 *Edinburgh*

This little guide for the location on the surface of the body of deeper lying anatomical structures will probably be found most useful by medical students in connection with their training in physical diagnosis. The entire omission of illustrations is a defect. There is a detailed index.

STUDIES ON THE MORPHOLOGY AND MORPHOGENESIS OF HUMAN THORACOPAGIC MONSTERS. With Special Reference to the Malformation of the Heart.

By *Fredrik Ysander Almquist and Wiksells*
Swedish Kr. 5 *Uppsala, Sweden*

6 x 9; viii + 236; 11 plates (paper)

This inaugural dissertation contains a detailed description of eight specimens of early human thoracopagic monsters; a summary of the reports of such double monsters in the literature between 1911 and 1922; and a discussion of the morphology and morphogenesis of these monsters. It is illustrated with 11 photogravure plates.



PHYSIOLOGY

HELMHOLTZ'S TREATISE ON PHYSIOLOGICAL OPTICS. (Translated from the Third German Edition) Vols. I, II and III.

By *H. von Helmholtz. (Edited by James P. C. Southall.) The Optical Society of America*
\$7 per volume; *Ithaca, N. Y.*
\$21 per set.

$7\frac{1}{2} \times 10\frac{3}{4}$; Vol. I, xxi + 482

Vol. II, viii + 480

Vol. III, x + 736

(Orders should be sent to F. K. Richtmyer, Secretary of The Optical Society of America, Rockefeller Hall, Ithaca, N. Y.)

The Optical Society of America has done a useful service to physiology by making available for the first time a complete translation in English of Helmholtz's great classic on physiological optics. The translation is from the third and definitive German edition which originally appeared in the years 1909 to 1911. In three large and stately volumes,

well printed and well bound, it should find a place on the shelves of every physiological laboratory. The translators have wisely adhered to the German text in the form in which it was left in the third edition, attempting to bring the material up to date only in the following ways: First, by the addition of a chapter on ophthalmoscopy, by Gullstrand; second, by the addition of several special contributions by von Kries; third, by the insertion of an article by Christine Ladd-Franklin on her theory of color; and, finally, by the addition throughout the entire work of some references to recent literature. In the main, however, the bibliographic references are left about as they were in the third German edition.

The distribution of the material in the three volumes is as follows: Volume I contains, first, an anatomical description of the eye, followed by Part I of the physiological optics, dealing with the dioptrics of the eye. Volume II discusses the sensations of vision, and Volume III the perceptions of vision.

Indices covering 29 pages complete the work. The translation and editing of this monumental work appear to have been done with great critical care and excellent judgment.



HUMAN METABOLISM WITH ENEMATA OF ALCOHOL, DEXTROSE, AND LEVULOSE. (*Publication No. 369.*)

By Thorne M. Carpenter

Carnegie Institution of Washington

\$2.25 6½ x 10; ix + 197 (paper)

Washington, D. C.

This extremely detailed account of a long experimental research shows that alcohol injected rectally is retained by the body and enters into its tissues, the

absorption being over 98 per cent. Studies of the alcohol in urine in short periods indicate that the utilization of alcohol is practically complete at the end of five hours, and is very high in the first one and one-half hours. The proportion of the total metabolism due to alcohol injected may be as high as 51 per cent. The utilization of alcohol in rectal feeding plays a prominent rôle in the total metabolism.



RECENT ADVANCES IN PHYSIOLOGY.

By C. Lovatt Evans

P. Blakiston's Son and Co.

\$3.50 5½ x 8½; xi + 364 *Philadelphia*

We cannot too highly recommend this book to our readers. In the words of its author "Its aim is to present to the student who has worked through an ordinary text-book an account of some of the problems with which physiologists have been concerned during recent years, and thus to serve, not only to enrich the student's knowledge as regards subjects of contemporary interest, but also to form a convenient bridge by which he may, if he feels so disposed, pass more easily into the original literature of those subjects." This highly intelligent and useful purpose has been extremely well accomplished by Dr. Lovatt Evans. The intriguing nature of the contents is apparent from their mere enumeration: Blood; Corpuscles and plasma; Suspension stability of blood; Origin of the blood cells, and their relation to the connective tissues; Fate of the red corpuscles; Carriage of carbon dioxide by the blood; Reaction of the blood; Output and work of the heart; Capillary circulation; Mechanism of tissue oxidations; Chemistry of muscular contraction;

Physical aspects of the physiology of muscular contraction; Application to the physiology of muscular exercise in man of the results of researches on the chemistry and physics of contraction; Active principles of some endocrine organs: thyroxin, pituitary principles, insulin; Mechanism of postural reflexes and the function of the labyrinth; Conditioned reflexes.

Adequate bibliographies of recent work follow each chapter. It is difficult to pick out for special mention any particular chapter of a book of such uniform excellence, but the final one on Conditioned Reflexes seems to us a masterpiece of clear and interesting scientific exposition.



LECTURES ON NUTRITION. (*A Series of Lectures Given at the Mayo Foundation and the Universities of Wisconsin, Minnesota, Nebraska, Iowa, and Washington (St. Louis).*)

IV. B. Saunders Co.

\$2.50 5 $\frac{1}{2}$ x 8; 243 pp. Philadelphia

This series of semi-popular lectures by distinguished authorities in the field of nutrition deals with the following subjects: The measurement and significance of basal metabolism, by Francis G. Benedict; Problems of metabolism, by Graham Lusk; The proportions in which protein, fat, and carbohydrate are metabolized in disease, by Eugene P. DuBois; Muscular activity and carbohydrate metabolism, by Archibald V. Hill; Our present knowledge of the vitamins, by Elmer V. McCollum; The Relations between fertility and nutrition, by Herbert L. Evans. Fairly extensive literature lists follow each chapter. The book will be useful for collateral reading in courses in general biology and physiology. Also the lay reader will find it a satisfactory

means of getting in brief space a wide ranging view of the present state of knowledge regarding nutrition.



A COLLEGE TEXT-BOOK OF PHYSIOLOGY.

By Arthur D. Bush Lea and Febiger
\$3.50 5 $\frac{3}{4}$ x 8; xiii + 331 Philadelphia

This new textbook of human physiology is designed to fill the gap in the textbook literature of this field which has existed by reason of the lack of any book especially adapted for college rather than for high school or for medical students. It covers the ground well, and seems admirably suited to the purpose. There are brief but well chosen reading lists following each of the twenty-two chapters. The book closes with a short glossary and index.



BASAL METABOLISM. *Determination of the Metabolic Rate in the Practice of Medicine.*
By John T. King, Jr.

The Williams & Wilkins Co.

\$2.50 6 x 9; 118 Baltimore

This is a brief review of the literature on basal metabolism, with special reference to the importance of such a study in the practice of medicine. There is a bibliography covering some 15 pages, and the book is well illustrated and indexed. It seems likely to serve a useful purpose as an introduction to the subject.



THE PRINCIPLES AND PRACTICE OF ENDOCRINE MEDICINE.

By William N. Berkeley Lea and Febiger
\$4.50 6 $\frac{1}{4}$ x 9 $\frac{1}{2}$; xi + 368 Philadelphia

While primarily intended for physicians in active practice this book will be found useful to the student of general biology

interested in any aspect of endocrine physiology. It reviews succinctly, impartially, and therefore somewhat uncritically, the extensive literature of this field. There are scattered through the book a good many interesting clinical observations by the author himself. It is well indexed.



BIOCHEMISTRY

APPLIED BIOCHEMISTRY

By Withrow Morse W. B. Saunders Co.
\$7.00 6 $\frac{3}{4}$ x 9 $\frac{3}{4}$; 958 pp. Philadelphia

This new and imposing text-book of biochemistry is written with the medical student directly in mind. The underlying philosophy is that if the medical curriculum is not to become overloaded and unbalanced each ancillary science must present only such material as is definitely related to medicine as a whole. Acting on this principle the author has made this a text-book of biochemistry as *applied* to medicine. It is both a laboratory manual and a didactic treatise. There are over 250 illustrations, many of them of apparatus. The wisdom of including so many cuts from apparatus dealers' catalogues seems doubtful. It is not unreasonable to suppose that a medical student already knows what an Erlenmeyer flask looks like. If he does not, he is certain to find out in the laboratory. Noteworthy features of the book are the great number of structural formulae given, and the series of portraits of living American biochemists. Since the book is intended strictly as a teaching manual, the final verdict as to its usefulness must rest with the experience of teachers. It has a detailed index.

CHEMICAL PATHOLOGY. (*Being a Discussion of General Pathology from the Standpoint of the Chemical Processes Involved.*)

By H. Gideon Wells W. B. Saunders Co.
\$8.50 6 $\frac{1}{4}$ x 9 $\frac{1}{4}$; 790 Philadelphia

In this fifth edition of the standard work on the chemical aspects of pathology the entire material has been worked over anew and the book rewritten. The size has been kept about the same as in the previous edition, largely by the expedient of dropping elementary material for which there is no longer need in such a book on account of the development of the teaching of biochemistry to medical students, and its replacement by new material marking recent developments of the subject. As a text-book for the medical student and a reference work for the general biologist, this work stands in the first rank.



LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. In 75 Vorlesungen. Für Studierende, Ärzte, Biologen und Chemiker. I Band: Organchemie. I Lieferung: Bausteine des Organismus—Blut. Vorlesung I Bis XVI.

By Prof. Dr. Otto Fürth F. C. W. Vogel
15 marks Leipzig

7 x 10; xiii + 208 (paper)

This is a revised edition, brought up to date, of the author's well known lectures on the problems of physiological and pathological chemistry. Its appearance has been delayed by the War. In its revised form the book will consist of two volumes in six *Lieferungen*. This first *Lieferung* deals with the following subjects: Protoplasm and the characteristics of the proteins; Aliphatic elements of the protein molecule; Cyclic elements of

the protein molecule; Hydrolytic splitting; Oxidative degradation of protein; Albumoses and peptone; Polypeptids; Carbohydrates; The simple fats and phosphatides; Cholesterin; Nucleic acid; Blood clotting; Blood serum; Haemoglobin; Haematin and its derivatives; Lymph, exudates and transudates.



BRIGHTER BIOCHEMISTRY. *Being the Illustrated Journal of the Biochemical Laboratory, Cambridge. No. 3.*

By D. M. Needham, M. G. L. Perkins, M. D. Whetham.

The Sir William Dunn Institute
2s. 6d. *Cambridge, England*

6 $\frac{1}{4}$ x 10; 64 (paper)

This year's volume of Brighter Biochemistry is good fun, as usual. The fooling is always pointed and sometimes extremely clever. Paradoxically Brighter Biochemistry tends to arouse serious and somewhat uncomfortable reflections on this side of the water. The deadly and devastating seriousness with which the American graduate student, statistically speaking, naturally takes every aspect of his life and his work seems somehow more pitiful than ever with B. B. in one's hand. And the worst of it is that all too often the only slogan that he ever hears from his professors is that well-known and greatly over-rated one about life being real and earnest.



SEX

HYGIENE OF SEX.

By Max von Gruber

The Williams & Wilkins Co.
\$1.50 5 x 7 $\frac{1}{2}$; xii + 169 *Baltimore*

The topics discussed in the nine chapters of this book are as follows:

Fertilization; Heredity and breeding; The organs of sex; The sexual instinct and the assumed necessity of coitus for health; The results of sexual excess and rules for the marital sexual intercourse; The limitation of conception; Aberrations of the sexual instinct; Venereal diseases and their prevention; Marriage or free love.

The real underlying philosophy of this treatise is indicated with entire fairness in the following quotations:

"Even the most sensual persons are not always sexually stimulated. Stimulation occurs only intermittently, as a rule only as a result of external influences, and it disappears spontaneously after a certain period if the external cause ceases to be operative" (p. 86).

"Manifestly, this discussion suggests that much can be done to prevent these stimuli. One can avoid drinking large amounts of fluid in the evening. One can take care to keep the bowels regulated. One may wear loose clothing and avoid the excessive pressure on the sexual organs by crossing the legs or by heavy bed clothes. One can prevent all unnecessary contact of the sexual organs with the hand. Washing and bathing will cleanse the skin. Medical care can be given early to skin eruptions, etc." (pp. 87-88).

"Mild disturbances and uncomfortable sensations, like restless sleep due to erection of the penis, and the frequent discharge of semen, headache and a conscious nervous tension can, as a rule, be easily avoided through the application of the methods previously mentioned. A moderation in eating, abstinence from alcoholic drinks and strongly seasoned food, a cool and not too soft bed, washing and bathing in cold water, and, particularly, an abundance of physical exercise, even to the point of fatigue, will be found to be definitely helpful. The con-

sistent avoidance of all those things which stimulate the sexual instinct renders abstinence the more readily accomplished, and, indeed, as we have already said, for this there is a physiological basis, since with lack of use of the sexual apparatus the testes curtail their activity" (pp. 93-94).

To complete the consideration of this antiquated, anaemic, academic, and asinine treatise, the following points seem relevant and worthy of record: (1) In 1925 the author was 72 years old; (2) 300,000 copies of the German edition were "sold abroad"; (3) *Ecce jam Europa!*



BIOMETRY

PELLIPLANIMÉTRIE. (*Mesure de la Surface du Corps Humain et Autres Corps.*)

By Dr. B. Roussy Gaston Doin et Cie
3 francs $5\frac{3}{8} \times 8\frac{1}{2}$; 27 (paper) Paris

This pamphlet is a succinct résumé of the author's original contributions to the problem of the measurement of the surface area of the living body. All students of anthropometry and metabolism will find it stimulating and interesting.



PSYCHOLOGY AND BEHAVIOR

DWELLERS IN THE JUNGLE.

By Lieut.-Col. Gordon Casserly

Ward, Lock and Co., Ltd.
5 shillings $6\frac{1}{2} \times 8\frac{1}{2}$; 255 London

These nature stories fall in manner somewhere between William Beebe and Rudyard Kipling. They are fascinatingly interesting and seem to be based upon extensive observation of animals in the

Indian jungles. They deal respectively with a baby elephant, langur apes, the jungle fowl, wild dogs, a crocodile, the weaver bird, a pet monkey, and a female elephant. We commend the book highly to anyone who loves nature or has children.



TASTSINN, STRÖMUNGSSINN UND TEMPERATURSINN DER TIERE UND DIE DIESEN SINNEN ZUGEORDNETEN REAKTIONEN. (*Zoologische Bausteine, Band 1, Heft 1.*)

By Konrad Herter Gebrüder Borntraeger
G. M. 12 $6\frac{1}{2} \times 10$; iv + 182 Berlin

This book, the first in a new series, is a careful compilation of what is known about the reactions of lower animals to tactile, current (both air and water) and temperature stimuli. There is a bibliography of 343 titles and a detailed index. It will be a useful work of reference to all students of animal behavior.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

IS IT GOD'S WORD? (*An Exposition of the Fables and Mythology of the Bible and the Fallacies of Theology.*)

By Joseph Wheless Wheless Publishers
\$4.00 105 West 40th Street,

$6\frac{1}{2} \times 9\frac{1}{2}$; xxv + 475 New York City

The writer of this extraordinary book is a distinguished lawyer. His purpose is to present a detached, calm, and in fact truly scientific, analysis of the Bible as a whole.

"No man, priest, parson, or zealot for his inherited faith, can say with truth that this book 'attacks the Bible,' or seeks to defame the Bible God or to ridicule the Christian Religion. If such

results follow, the Bible itself is to blame, if this book of mine speaks truly. This book is based wholly on the Bible; its all but every reference and citation is to the texts of the Bible, faithfully quoted in exact words of inspiration. The Hebreo-Christian God is depicted in the plain words of revelation for his every word and deed attributed to him by the inspired writers. This book is simply the Bible taken as a whole, and thus viewed in a light not shed upon it by pulpit expoundings of golden texts or private casual readings of isolated choice fragments.

'If the Bible and its derived dogmas suffer from this simple process of 'searching the Scriptures whether these things were so,' the fault, dear reader, is not in the candid writer of this book, but in The Book, which utters the things which are simply and truly quoted and compared, in simple juxtaposition of contradictory texts, and not in the usual isolated and scattered passages as is the custom of sermons and pious tracts. Here is my book; there lies the open Bible; any man who will read, and is curious or interested for the truth, may judge wherein is the truth" (pp. xxiii-xxiv).

The results of this simple and novel procedure, which is carried out with good judgment, a modicum of humor, and an entire absence of rancor, may fairly be called stupendous. We commend the book in the strongest terms to our readers because we believe that probably few of them have any *adequate* conception of just what kind of a book the Bible really is. A more effective answer to fundamentalism than Mr. Wheless' treatise is inconceivable.

We are informed that the publication of this important book has been taken over by Alfred A. Knopf, Inc.

LANDMARKS IN THE STRUGGLE BETWEEN SCIENCE AND RELIGION.

By James Y. Simpson George H. Doran Co.
\$2.00 5½ x 8; xv + 288 New York

J. W. Draper's *The Conflict between Religion and Science*, and Andrew D. White's *A History of the Warfare of Science with Theology in Christendom*, are the classic works in the field they cover. Neither has ever been successfully controverted in respect either of its main facts or conclusions. The present book covers essentially the same ground, but its attitude leans much more sympathetically towards the religious side of the controversy than is the case with either of its predecessors. Mr. Simpson's egg was boiled a very much shorter time than either Mr. Draper's or Mr. White's.



MATTER, MAN AND MIND.

By W. F. F. Shearcroft The Macmillan Co.
\$3.00 5½ x 8½; 191 New York

This entertaining and well-written volume wanders widely over the whole range of science, but with a great deal more emphasis upon biological than upon physical matters. It ought to have a wide popular appeal. Its science is sound, its style has clarity and real charm, and it avoids the blatancy of the yellow journal, which in America is rapidly coming to be regarded as the highest ideal of popular scientific writing.



RELIGION AND NATURAL SCIENCE.

By E. Haigh Student Christian Movement
4s. 6d. 5½ x 8; xi + 170 London

This is a religious tract written by a secondary school teacher of physical science. Its obvious purpose is to keep

bright young boys and girls, who may chance to become interested in science, from straying out of the safe and pleasant fold watched over by the pastor. We are told that "Faith is not a weaker kind of knowledge, a sort of crutch to lean upon when our footing is not secure. It is the exercise of a higher faculty than the intellect" (p. 117).



HOMÖOPATHIE. *Kritische Gänge Hüben und Drüben.* (*Moderne Biologie* Heft 10.)

By Prof. Dr. Hans Much Curt Kabitzsch
4.20 marks 5 x 7½; 142 Leipzig

A welcome candidate to the Budget of Biological Paradoxes. It is a quasi-philosophical discussion of what homeopathy is, what it is not, and what it should be in the light of modern biological knowledge.



DISEASE PREVENTION.

By Herbert H. Waite Thomas Y. Crowell Co.

\$4.50 6 x 9; xi + 667 New York

This treatise on preventive medicine

strictly follows the conventional lines. Its interest would have been enhanced by illustrations and by greater conciseness. Its chief usefulness seems likely to be as a convenient reference work.



THE AMERICAN ILLUSTRATED MEDICAL DICTIONARY. (*A New and Complete Dictionary of the Terms Used in Medicine, Surgery, Dentistry, Pharmacy, Chemistry, Nursing, Veterinary Science, Biology, Medical Biography, etc., with the Pronunciation, Derivation, and Definition, Including much Collateral Information of an Encyclopedic Character.*)

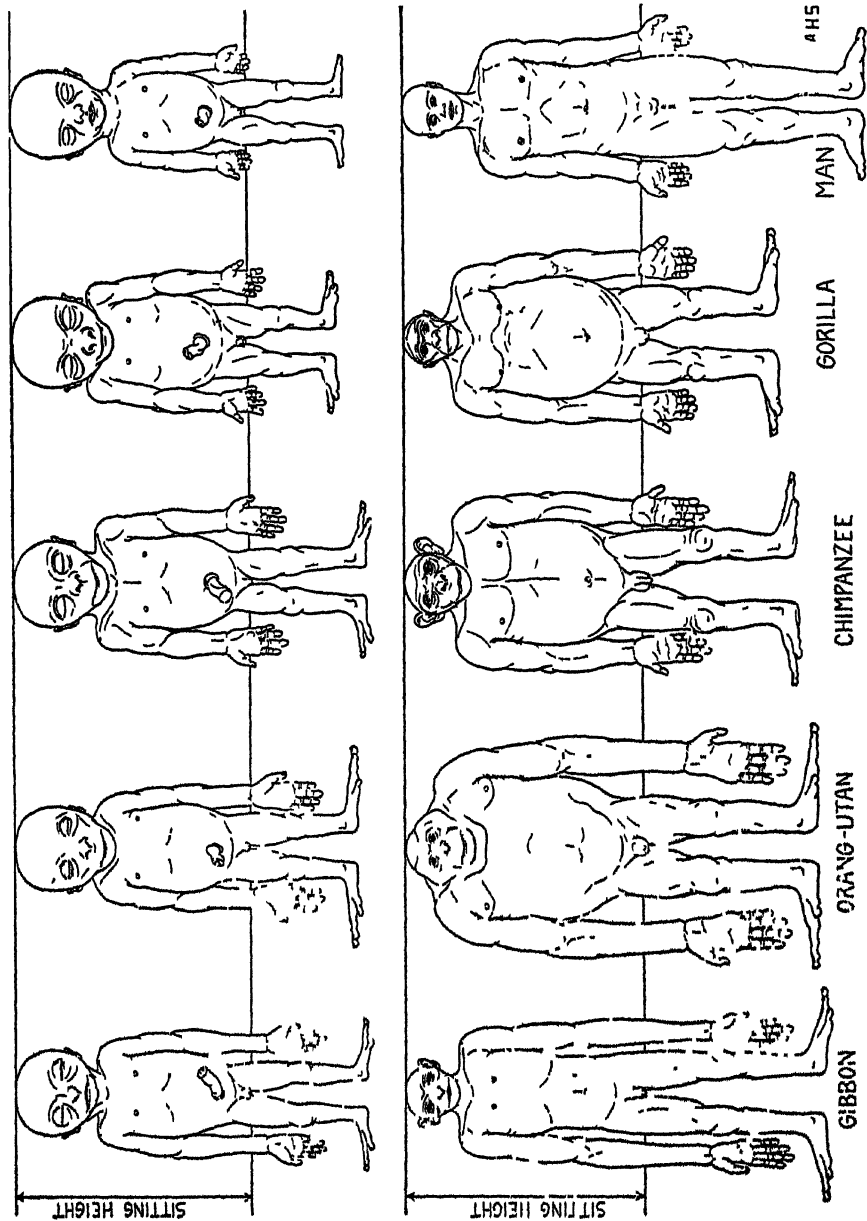
By W. A. Newman Dorland

W. B. Saunders Co.

\$7.00 6½ x 9; 1344 Philadelphia

The thirteenth revised and enlarged edition of this well-known and thoroughly established medical dictionary contains about 2500 new words. Dorland's Dictionary is a never failing resource to the biologist who finds himself entangled in the intricacies of medical technicalities.





DIAGRAMMATIC REPRESENTATION OF THE BODY PROPORTIONS IN APES AND MAN OF FETAL AND ADULT GROWTH STAGES

The fetuses (above) are arranged in the same order as the adults (below). All the figures have the same sitting height. The human fetus is of the 4th month, the gorilla and the gibbon fetus correspond in development to the human fetus, but the chimpanzee and the orang fetus are slightly more advanced in their growth. The figures for chimpanzee and gorilla have been constructed from measurements and photographs in the literature.

THE QUARTERLY REVIEW *of* BIOLOGY



FETAL GROWTH OF MAN AND OTHER PRIMATES

By ADOLPH H. SCHULTZ

Laboratory of Physical Anthropology, Department of Anatomy, Johns Hopkins University

I. INTRODUCTION

WHEN human growth is divided into an embryonic, a fetal, and a post natal period, it is found that our knowledge in regard to the first and last parts is far more advanced than that of the middle or fetal period. Of all biological sciences embryology and physical anthropology have contributed the largest shares to the literature on human growth. The physiology and the histology of growth have been investigated much less and not until in comparatively recent years, the latter for instance by Levi (1925), the former by Friendenthal (1914). Comparative studies on the growth of different animals have been undertaken for but few and special purposes and no comprehensive paper on this promising problem is available as yet. In short, it can be stated that of the multitude of questions, arising from the study of growth, a large proportion has up to the present time either not been answered at all or only in a tentative and incomplete manner.

This review is restricted almost entirely

to observations from the field of physical anthropology and places main emphasis on the period of growth extending from the time the embryo has gained a definitely human form to birth. In other words, the following discussion will deal principally with those ontogenetic changes in body size and proportions which take place during that phase of development which links the period properly assigned to embryology with that covered by the enormous literature on growth in children (Baldwin (1921) has collected 911 titles pertaining to the growth of man from birth to maturity). Conditions in juveniles and adults are mentioned in this paper merely in order to indicate the general trend of growth changes during life after birth, and to compare certain features of fetal development with those at later stages of growth.

Literature

As mentioned before, the literature on human fetal growth is, relatively speaking, not very extensive. The majority of the papers have a very limited scope, dealing only with the weight and some

few main dimensions of the fetus. Detailed investigations on fetal body proportions are with few exceptions based upon insufficient material, from a study of which it has been rarely possible to arrive at the typical, representative conditions. Individual variations are fully as frequent and pronounced before birth as in later stages of growth, as shown, for instance, by Fischel (1896) and Mehnert (1896) for vertebrates in general and by the author (1926c) for man in particular. To examine large numbers of individuals is, therefore, as essential for conclusions on prenatal development, as it was always deemed absolutely necessary in work on the growth of children.

Little could be gained here by attempting an exhaustive review of the literature on fetal growth in man. This would require an undue amount of space, in which to enumerate and analyze the many discrepancies—often due to inaccurate technique—in the results of the older investigators. Therefore, only some of the more important papers will be mentioned in this introduction, and reference to others will be made later on in connection with the particular problems on which they bear. The main part of this paper will be devoted to a presentation of final facts and of recent observations, while the varying and more or less hypothetical interpretations of these findings will be assigned a subordinate rôle.

The first problem of prenatal growth is the correlation between age and size of the developing organism. Data on this serve also in another fundamental problem, namely in the calculation of the rate of growth in the different periods of intrauterine life. Of the authors who have worked along these lines the following may be mentioned: Hecker (1866), Ahlfeld (1871), Fesser (1873), Calderini (1875), Henning (1879), Toldt (1879),

Hamy (1880), Preyer (1885), Faucon (1897), Daffner (1902), Loisel (1903), Michaelis (1906), Roberts (1906), Tuttle (1908), Stratz (1909 a & b), Jackson (1909), Mall (1910 & 1918), Zangemeister (1911), Weissenberg (1911), Friedenthal (1911), Meyer (1914 & 1915), and Streeter (1920). Very extensive and reliable data are contained in the paper by the last named author and it is upon this paper that the writer has based the age estimation of his material.

A number of attempts have been made, chiefly by Noback (1922), Scammon and Calkins (1923), and Arey (1925), to reduce various phases of fetal growth to mathematical formulae by introducing certain constants. In view of the above mentioned high variability during fetal life and for certain reasons, to be referred to later on, such formulae can represent only a rough approximation to the actual and complicated conditions of growth.

The fetal growth of the head has been studied particularly from the obstetrical point of view, as for instance by Legou (1903), León (1912), and Calkins (1922). Detailed investigations on the growth before birth of the limbs alone have been made chiefly by Bartscher (1877), Mendes Corrêa (1919), and Reicher (1925). A variety of measurements, covering all parts of the fetal body, have been published by Retzius (1904), who based his studies on a total of 87 specimens, by Reicher (1923), who had a series comprising 366 fetuses, and by the writer (1922 & 1923 b), who has examined a series of 623 fetuses.

Fetuses of different human races

Unfortunately there are as yet but few publications on fetuses of races other than the white. Friedenthal has described the fetus of a Papua (1913) and one of a negro (1914). Some few data on seven fetuses

of the latter race have been published by Hamy (1881). The writer (1920) has studied the prenatal development of the nose on a large series of negroes and on some Filipinos, American Indians, and Japanese, and in a later paper (1923 b) he gave a preliminary report on the general body proportions of 168 negro fetuses. Three recent papers deal with Japanese fetuses: Kudô (1923) gives data on the viscera of 111 specimens, Akiba (1924) measured certain proportions, particularly in regard to the limbs, on 160 fetuses, and Nishizuka (1925), in an excellent study on the development of the bones in the extremities of the Japanese (70 specimens of prenatal stages), lists a few fetal proportions.

Fetuses of apes and monkeys

The changes during growth in the size and proportions of the body, when studied in man alone, can mostly go little beyond a mere recording of the bare facts and allow but few conclusions as to the probable reasons underlying the changes. Many of the reasons, however, are suggested by comparing human growth with that in other animals, particularly other primates. For such comparative growth studies relatively little help is found in the literature. Not only have rather few data on fetuses of monkeys or apes been recorded, but the varying technique, employed by the different authors in measuring their material, renders exact comparison almost impossible. Some embryos and fetuses of various primates have been described (mostly with good illustrations, but with few, if any, measurements) by Kollmann (1892 a & b), Sclenka (1892, 1899, & 1903), Wiedersheim (1901), Frédéric (1905), Keibel (1906 & 1911), and Bluntschli (1913). Data on other specimens, including some detailed measurements, have been published by Trin-

chese (1870) for an orang-utan fetus, by Deniker (1884 & 1885) for a gorilla and a gibbon fetus, by Toldt (1903) for two macaque fetuses, by Duckworth (1904) for a gorilla fetus, by Schwalbe (1911) for 4 orang fetuses, 23 gibbon and siamang fetuses, and 67 Asiatic monkey fetuses, by Friedenthal (1914) for two chimpanzee fetuses, and by the writer (1921 b) for two howler monkey fetuses, (1924 a) for three Colobus monkey fetuses, and (1924 b) for 5 anthropoid fetuses, 12 gibbon and siamang fetuses, 25 fetuses of Old World monkeys and 24 fetuses of American monkeys. In addition to these prenatal stages use was made of 109 infantile, juvenile, and adult monkeys and apes. Detailed information on the different species and on all the measurements and observations obtained from this material will soon be published elsewhere. The species names, used in this paper, are according to Elliot (1913).

Recapitulation theory

It is evident from these references to previous work on the development of different human races and of the various monkeys and apes, that no complete picture of fetal growth in primates can be given as yet, since only for the white race of man are there anywhere nearly sufficient data available. However, these comparative studies have progressed far enough to establish at least some of the outlines for this new chapter of science, in which embryology, physical anthropology, and primatology coöperate and really overlap. These outlines promise to be very helpful for our understanding of the many widely diverging specializations in different primates, including man. It will be shown later on that a great many human racial differences are already apparent in the fetus. This is, of course, not restricted to man, but holds true also

in regard to other mammals. For instance, Lönnberg (1917) has shown that in elephant fetuses the racial characteristics are very conspicuous, and this comparatively early since one specimen of *Elephas africanus cottoni* Lydekker had a crown-rump length of only 305 mm. The writer found some of the distinguishing features of certain breeds of dogs well defined in fetuses. Most of the peculiarities of the different monkeys and apes are clearly indicated before birth. However, racial differences, as well as the distinguishing characters of man and apes are less pronounced in early than in late growth stages; indeed, in embryos the similarity of certain body parts may at times verge on identity. As extreme specializations were not yet present in earlier evolutionary stages of the species, so are they lacking in early growth stages of the individual. This constitutes one of the main supports for the well-known and much contested recapitulation theory, according to which ontogeny (or individual development) repeats phylogeny (or the evolution of the species). This theory, which, at its inception, was even called a law, can not be taken literally and is to be applied with great caution. Theoretically it should be regarded as a working hypothesis and thus as a constant challenge for a possible other, and perhaps more satisfactory, explanation. However, the apparent exceptions to this theory, which have been quoted in the past in attempts to discredit it, appear to the author merely as evidence of the many other natural agencies which interfere with the exclusiveness of the principle of recapitulation by superimposing themselves on the latter.

In the search for the causes of ontogenetic changes the writer has always endeavored to look first of all for possible explanations other than those involving

any phylogenetic speculations. However, if no direct causation offers itself, one is simply compelled to interpret the change as a phyletic contraction and by this is meant the inherited passing (or sometimes even permanent) re-appearance of a condition having existed in ancestral forms at some period of their growth. A great many phenomena of growth could not be understood to-day without at least this conservative version of the recapitulation theory. The tremendous amount of literature for and against this fundamental theory can not be discussed in this connection, but readers are referred at least to the critical essay by Naef (1917) and to the conclusions of Peter (1920) in regard to limiting and modifying influences on "recapitulation."

II. METHODS OF INVESTIGATION

All the detailed methods for the anthropological study of fetal growth will be described in full in another paper by the author which is to appear soon in the Contributions to Embryology (Publications of the Carnegie Institution of Washington). The justification of particulars in the technique chosen by the author, the necessary instruments, and the mathematical treatment of the data obtained will also be completely discussed in this future paper.

Since, however, the present paper deals chiefly with the ontogenetic changes in the size and proportions of the body some brief remarks have to be made in regard to the technique of measuring. To neglect this, as so many former authors have done, would render the data to be presented useless or at least unreliable for future comparative studies.

The measurements on fetuses correspond, wherever possible, in every detail to those in general use on adults. The latter have been described in full by Martin (1914).

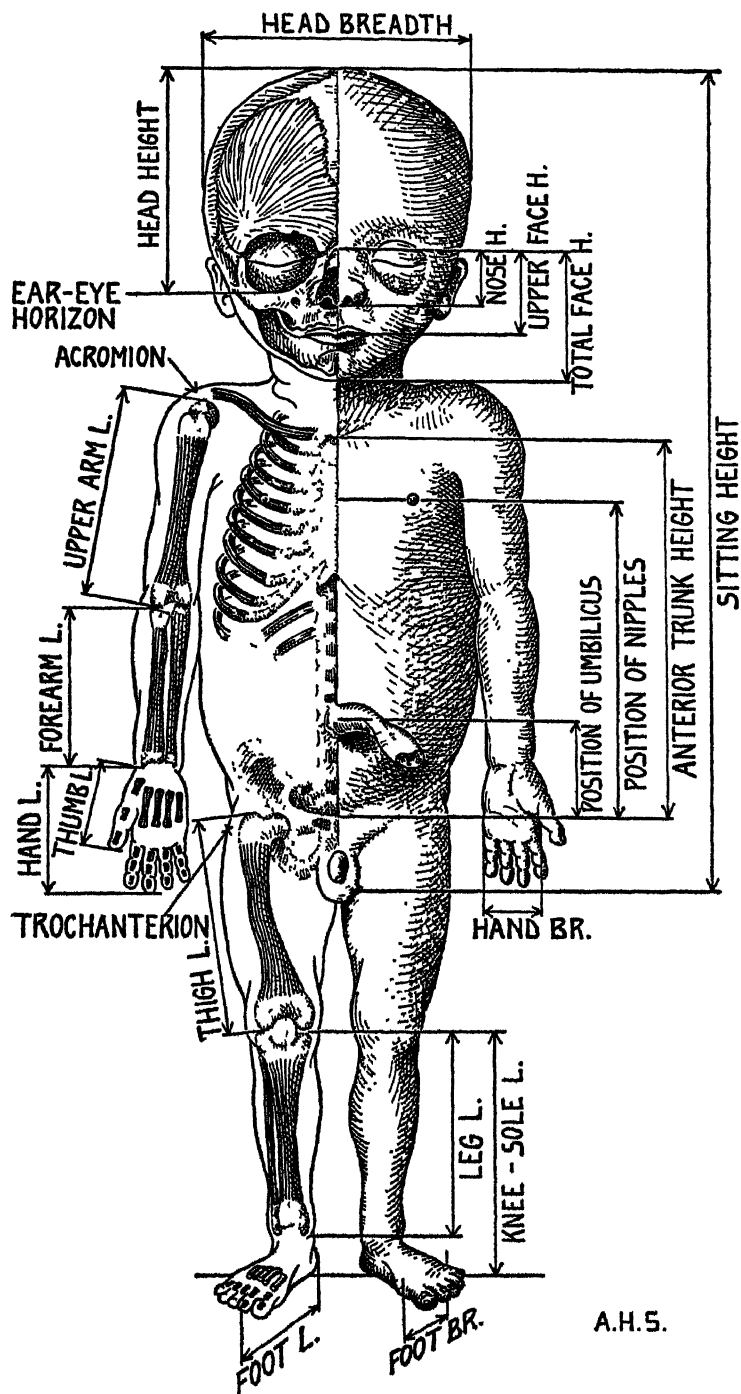


FIG. 1. DIAGRAMMATIC REPRESENTATION OF THE MEASUREMENTS TAKEN ON HUMAN FETUSES
The essential parts of the skeleton are shown on the right half of the fetus

Figure 1 gives in a diagrammatic way most of the measurements on fetuses and shows that the majority of these are determined by the underlying structures of the skeleton. The figure is self-explanatory, so that it only remains to describe a few additional measurements which could not be drawn in. The total head height is the distance from the vertex to the chin (perpendicular to the ear-eye horizon). The head length is taken from the glabella to the most distant point on the occiput. The horizontal head circumference is also determined by these last mentioned points. The face breadth is the greatest width between the zygomatic arches. The interocular breadth is the width between the inner angles of the eye clefts. The nose breadth represents the greatest width between the nasal wings. The cephalothoraco-abdominal height is the distance between the upper edge of the symphysis pubis and the vertex. The stature is obtained by adding to the last measurement the thigh length and the knee-sole length. On fetuses and in primates the lower limbs can not be straightened without injury to the specimen and the stature can therefore not be measured directly but has to be a composite measurement. The symphysion-acromion height is the distance from the upper edge of the symphysis pubis to the middle of a line connecting the two acromion points. The height of the shoulder over the suprasternal notch is the difference between the last measurement and the anterior trunk height. The above mentioned line between the two acromial points constitutes the shoulder (or biacromial) breadth. The lower width of the trunk, or the hip (bitrochanteric) breadth, is the distance between the two trochanterion points, which overlie the most lateral points of the great trochanters. Finally, the sagittal and transverse diameters of the chest

and the horizontal chest circumference are taken at the level of the fourth pair of ribs, where this meets the sternum.

With these measurements it is possible to construct complete and accurate diagrams of the body proportions of any specimen or, from the average measurements, of the type for any growth stage (see e.g., the frontispiece to this paper).

The absolute size of the various body parts is of less importance in a discussion of growth than their relative size or proportions. The stature is most commonly used as the standard in percentage of which other measurements are figured. However, the total body height is really not a morphological unit and can only be satisfactorily taken in children and adult man. In other mammals, in which the posterior extremities are more or less bent toward the trunk, no one would think of combining the height of the head with the length of the neck and trunk and that of the posterior limb in one measurement. This fact that the standing height of man is composed of so entirely different units limits its value as a standard for relative measurements to few and special purposes, such as racial studies on adults. One of the few real justifications, even in racial studies, for expressing measurements in relation to stature is the fact that nearly all the previous data on adult man are recorded in this way. Plitzner (1899) and Mollison (1911) have expressed themselves even more emphatically against the use of stature as a basis for relative measurements. In work on growth and in comparative investigations on different primates the most suitable standard is the sitting height, or, better still, the anterior trunk height. The latter measurement characterizes the development in length of the trunk. This constitutes the closest approach to a perfect standard for the main body proportions.

The relations in size between the limbs or the head and the trunk are unquestionably more important than the proportion between, e.g., the lower limb length and the stature, of which the first measurement itself forms a large and very variable part.

upon stature. No general rule can or should be proposed as a guide for the many detailed proportions; these are determined by the particular problems to be solved.

The source of technical error in measuring small fetuses is not necessarily greater

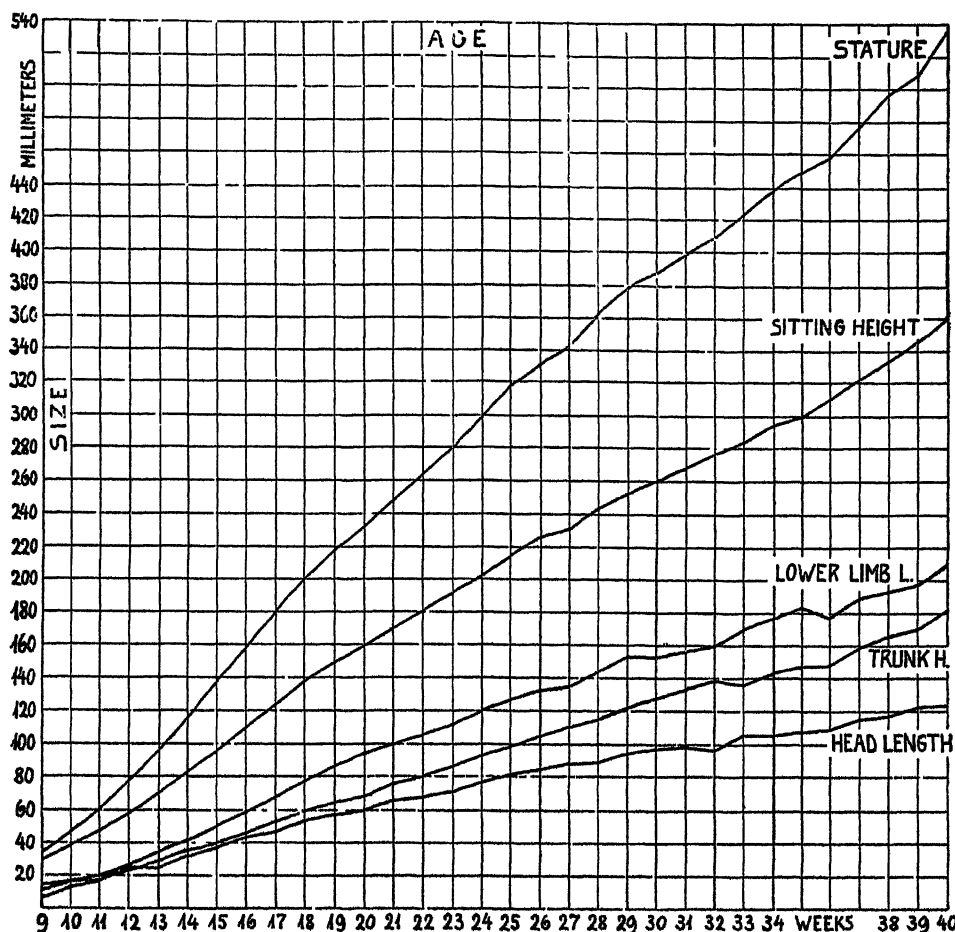


FIG. 2. CURVES OF GROWTH FOR STATURE, SITTING HEIGHT, LENGTH OF LOWER LIMB (GR. TROCHANTER TO SOLE), ANTERIOR TRUNK HEIGHT, AND HEAD LENGTH OF WHITE FETUSES (9 WEEKS TO BIRTH)

Furthermore, the relations between the limbs, or head, and stem can be directly compared in all different growth stages and in all primates, or in even widely different groups of mammals, whereby the typical differences are far more clearly brought out than in proportions based

than in measuring the living adult, since on the dead fetuses one can readily control the determination of the points of measurement by the aid of fine pins or even by dissecting the soft parts over the skeleton, wherever the latter can not be palpated on the surface with absolute certainty. The

preservation of fetuses introduces a possibility of artificial changes, as was shown by the author (1919) on some special experiments. However, more than 96 percent of the material, used in this study, was preserved uniformly in 10 percent formalin, so that the error through different preservation can be considered as negligible for all practical purposes. The error in consequence of the slight swelling of the tissues in the preserving fluid must affect the entire series in a similar way and thus can exert but a very insignificant influence upon proportions and their fitness for comparison.

All the absolute measurements in this paper are given in millimeters. The fetal age is stated in weeks or in lunar months (4 weeks each) and represents the so-called menstrual age.

III. RATES OF GROWTH

Age and growth rate

The human body grows at entirely different rates in different periods of its development; in general it can be said that this rate of growth diminishes very rapidly with advancing age. The fertilized ovum has an approximate weight of 0.005 milligrams (Meyer, 1914), at the beginning of fetal life (9th week) the body weighs roughly 1.1 grams (Streeter, 1920), which means that during embryonic development the weight is increased for 220,000 times its initial amount. If the average weight of the white newborn is placed at approximately 3200 grams, the increase during fetal growth equals 2,900 times the weight at 9 weeks. Finally, during life after birth the weight of the newborn is increased only about 20 times. In relation to time these growth rates are even more strikingly different, since embryonic life lasts roughly 8 weeks, fetal life 32 weeks, and postnatal growth about

1000 weeks. In the first period the weight increases on an average per week 27,500 times, in the second or fetal period 90 times, and in the last growth period only 0.02 times.

Growth rates in different parts of the body

The absolute growth during fetal life of some of the more important body measurements is shown by the curves in figure 2. These dimensions, naturally, increase at a much slower rate than the

TABLE 1
Averages for the proportion: Stature in percentage of sitting height

9 weeks	115.8	26 weeks	146.7
10 weeks	126.4	27 weeks	147.3 148.3
11 weeks	128.6 130.0	28 weeks	148.3 151.6
12 weeks	132.4 132.6	29 weeks	149.2 151.1
13 weeks	138.0 135.4	30 weeks	148.0 149.0
14 weeks	139.7 140.7	31 weeks	148.7 150.2
15 weeks	142.4 141.8	32 weeks	148.0 147.3
16 weeks	142.6 144.0	33 weeks	149.2 148.9
17 weeks	144.0 143.8	34 weeks	147. 148.8
18 weeks	144.4 143.0	35 weeks	148.8 150.4
19 weeks	146.0 147.0	36 weeks	146.9 146.7
20 weeks	146.4 146.9	37 weeks	147.5 151.4
21 weeks	146. 145.6	38 weeks	148.0 148.9
22 weeks	146.5 148.5	39 weeks	146.2
23 weeks	147.2 149.0	40 weeks	
24 weeks	148.0 149.0	Adults	201.7
25 weeks	148. 148.2		

weight; e.g., the stature amounts on an average to 32.7 mm. in the middle of the 9th week and to 532.1 mm. at birth, an increase of only 16.3 times the initial value. The different curves do not proceed in a constant relation to each other, but manifest a certain independence. This is best shown on the example of the percentage relation between stature and sitting height, which is given in table 1. At 9 weeks of fetal life the standing height exceeds the sitting height by only 15.8

percent of the latter, at the end of the 6th month the former measurement is nearly one and a half times as long as the latter measurement, and in adults the stature equals about twice the sitting height. In other words, the total body height grows much faster than the sitting height from the 9th to the 15th week of fetal life and

negroes have the slightly higher values, is already clearly indicated in fetuses, since in 22 week groups the negro fetuses have higher averages than the white fetuses, whereas in only 9 groups is this relation reversed. The higher this index the relatively longer are the lower extremities. This racial difference means,

TABLE 2

Monthly averages of the relative weekly increments in some body dimensions of white fetuses. The relative weekly increment is obtained by expressing the difference between the averages of a given measurement in two successive weeks (absolute weekly increment) in percentage of the smaller average

MEASUREMENT	3RD MONTH	4TH MONTH	5TH MONTH	6TH MONTH	7TH MONTH	8TH MONTH	9TH MONTH	10TH MONTH
<i>General:</i>								
Standing height.....	32.6	19.8	10.5	6.5	5.1	3.0	2.7	4.0
Sitting height.....	26.7	17.6	9.7	6.4	4.9	3.1	3.0	3.8
<i>Trunk:</i>								
Trunk height.....	29.2	18.0	9.5	8.2	5.7	5.0	1.6	5.3
Chest circumference.....	23.2	19.3	10.7	6.0	2.6	4.2	2.3	4.7
Shoulder breadth.....	24.3	19.3	11.1	6.2	4.8	3.4	2.5	6.2
Hip breadth.....	31.0	23.6	11.5	7.5	4.3	4.0	3.1	5.6
<i>Upper limb:</i>								
Total length.....	39.3	23.3	11.1	5.8	4.5	2.5	3.1	4.4
Upper arm length.....	44.5	23.2	10.3	5.2	4.0	2.1	2.9	4.4
Forearm length.....	46.4	24.0	10.9	5.3	4.0	2.6	2.5	4.9
Hand length.....	26.0	22.3	12.6	7.3	5.9	3.1	4.2	4.0
<i>Lower limb:</i>								
Total length.....	45.5	24.2	12.3	6.9	4.1	2.9	3.1	4.0
Thigh length.....	45.7	23.0	11.5	6.8	3.7	3.5	2.7	4.1
Leg length.....	48.7	26.5	12.6	6.7	4.4	2.4	3.3	3.6
Foot length.....	29.5	21.9	13.4	8.2	5.9	3.0	3.7	4.0
<i>Head:</i>								
Length.....	22.0	17.0	9.9	5.9	4.2	2.4	2.7	3.1
Breadth.....	22.2	17.4	8.7	5.1	3.5	3.6	2.3	2.3
Height.....	24.0	15.3	9.4	4.5	4.6	1.7	2.8	3.1
Horizontal circumference.....	24.9	16.6	9.4	5.8	3.6	2.8	2.8	2.6
Total face height.....	25.0	16.9	11.0	5.7	3.3	4.6	1.7	3.3
Face breadth.....	23.5	19.5	9.5	4.9	3.2	3.3	2.6	3.0

again during postnatal development. From the 15th to the 20th week the difference between the growth rates of these measurements is but little, and between the 6th month and birth the two grow about equally fast. Incidentally, table 1 shows also that the racial difference in this proportion, according to which adult

therefore, that negroes have in general proportionately longer legs than whites (see also Bean, 1922).

Fluctuations in growth rate

It has been shown above that in general the rate of growth diminishes very markedly with advance in age and that different

parts of the body grow at times with different intensity. Both these general rules, in their particular application to fetal growth, are very evident in the figures listed in table 2. The relative increments of all the various measurements are far higher in the first than in the last part of fetal life. However, the decrease in these increments is not quite continuous, since it changes in most measurements to a slight increase during the last few months before birth. Thus, the actually lowest rate of growth occurs in the

can here be mentioned, namely those by Zeising (1854) and by Bean (1923, 1924).

Alternations in growth rate

Besides these fluctuations there occur clear alternations in the growth rates of different parts of the body. For instance, as shown by table 2, the relative increments for the trunk height are greater than those for the chest circumference and shoulder breadth in the 3rd month of fetal life. In the 4th and 5th months this relation is reversed, only to change back

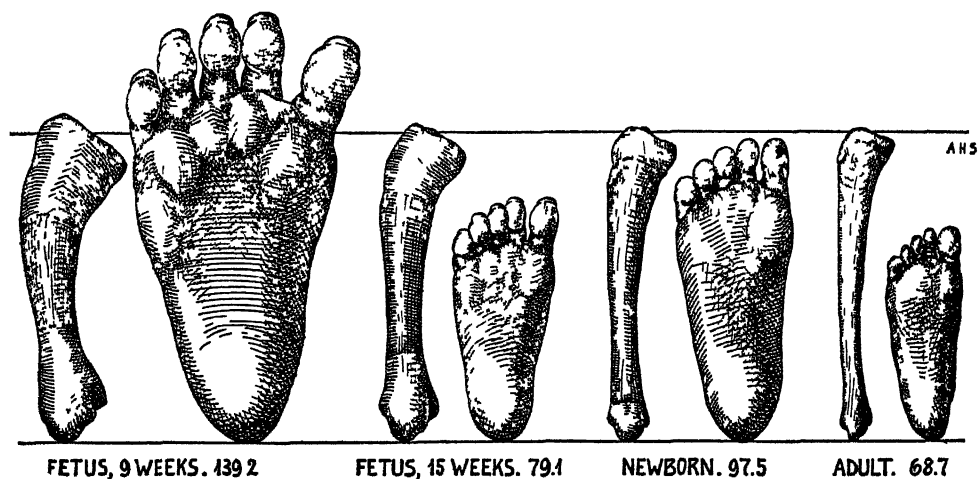


FIG. 3. SCHEMATIC REPRESENTATION OF THE RELATION BETWEEN FOOT LENGTH AND LEG LENGTH (LENGTH OF TIBIA) AT DIFFERENT GROWTH STAGES

All the tibiae have been drawn to the same length (= 100). The proportions of these drawings are based upon the averages of measurements on large series of whites.

stature, sitting height, and trunk measurements during the 9th month, in the majority of the limb measurements during the 8th month, and in most of the head measurements during the 8th or 9th month. This indicates a certain periodicity for fetal growth, similar to the well known fluctuations in the growth rates after birth which are not restricted to man, but are found in other animals as well (e.g. Gartner, 1922). Of the many papers dealing with the periodicity of postnatal growth only the first and last

again in the 6th, 7th, and 8th months, and to change a third time in the 9th and 10th months to a preponderance in rate of growth in width over that in height. Not only growth in height and width alternate in intensity—producing successive periods of “stretching” and of “filling”—but also growth in such adjoining parts of the body as the different segments of a limb. For instance, the most distal parts of the extremities, the hand and foot, grow more slowly than the more proximal parts during the 3rd and

the 4th months, whereas from the 5th to 9th month the relative increments of the upper arm and forearm surpass those of the hand and the increments of thigh and leg are larger than those of the foot. In a similar way alternate the growth rates in the trunk height and in the total limb lengths, the latter increasing faster than the former during the 3rd, 4th, and 5th months, but more slowly in the 6th, 7th, and 8th months and again in the 10th month, while in the 9th month it is once more the trunk which grows at the slower rate (see table 2). Such alternations in growth rate also take place during post-natal life, only there they are spread over much longer periods, which are reckoned in years rather than in months (e.g. Godin, 1903 & 1910 a).

These changes in the relation between the intensities of growth in different body parts determine directly the changes in the proportions during development. An illustration of this is given by figure 3 which shows the striking fluctuations in the proportion between the lengths of foot and leg. At 9 weeks of fetal life the human foot is very much longer than the leg, at 15 weeks the leg has become the longer of the two on account of the much slower growth rate in the foot than in the leg, but at birth both are nearly equal in length. During growth after birth the leg again increases faster than the foot, reducing the length of the latter to 69 percent of that of the former.

Growth rate and species differences

Different proportions in adult primates with divergent specializations can often be traced to differences in growth rates, as shown by the example in figure 4. In early fetuses the three segments of the upper extremity have practically the same proportionate lengths in man and gibbon; the middle segment at this time is the

shortest in both. In older fetuses the forearm has surpassed the hand in length in man and ape. Not until birth appears the peculiarity of the gibbon, i.e., a forearm exceeding in length the upper arm, and even then this is just barely indicated. The great lengthening in the upper extremity of the gibbon, which is unequaled in its proportionate amount by any other primate, takes place most of all in the forearm, but the excess of the latter over the upper arm becomes most pronounced only at the completion of growth. Thus, it can be said that it is primarily a difference in relative rate of growth which brings about the difference in the arm proportions between adult man and gibbon.

Law of developmental direction

This chapter on the rates of growth can not be closed without some brief remarks bearing on the so-called law of anteroposterior development (Child, 1915), or of cephalocaudal differential growth (Kingsbury, 1924, 1926) which is also called the law of developmental direction (Jackson, 1914). According to this law, the early differentiation of the embryo, as well as its later development, proceeds in general in all vertebrates in the head-to-tail direction, so that the more caudal parts of the body are for a considerable period a step behind the more cephalic parts in their development. This, for instance, is evident from the fact that the arm bud antecedes the leg bud in its appearance. This acceleration in the development of the upper extremity, or retardation in that of the lower extremity, is not confined to embryonic growth but clearly persists even to advanced stages of fetal life. Illustrations of this are furnished by the following notes from the author's observations on human fetuses: The separation of the fingers occurs earlier than that of the toes.

The touch pads on the hand can be either dimly recognized or have disappeared altogether in fetuses (of about 12 weeks) in which the plantar touch pads are still well defined. In many fetuses of about the 22nd week sparse and very short

bear already hairs of considerable length. The papillary ridges develop slightly sooner on the palm and fingers than on the sole and toes. Fetuses of the 6th month have ossified zones in all the middle phalanges of the fingers, but in the

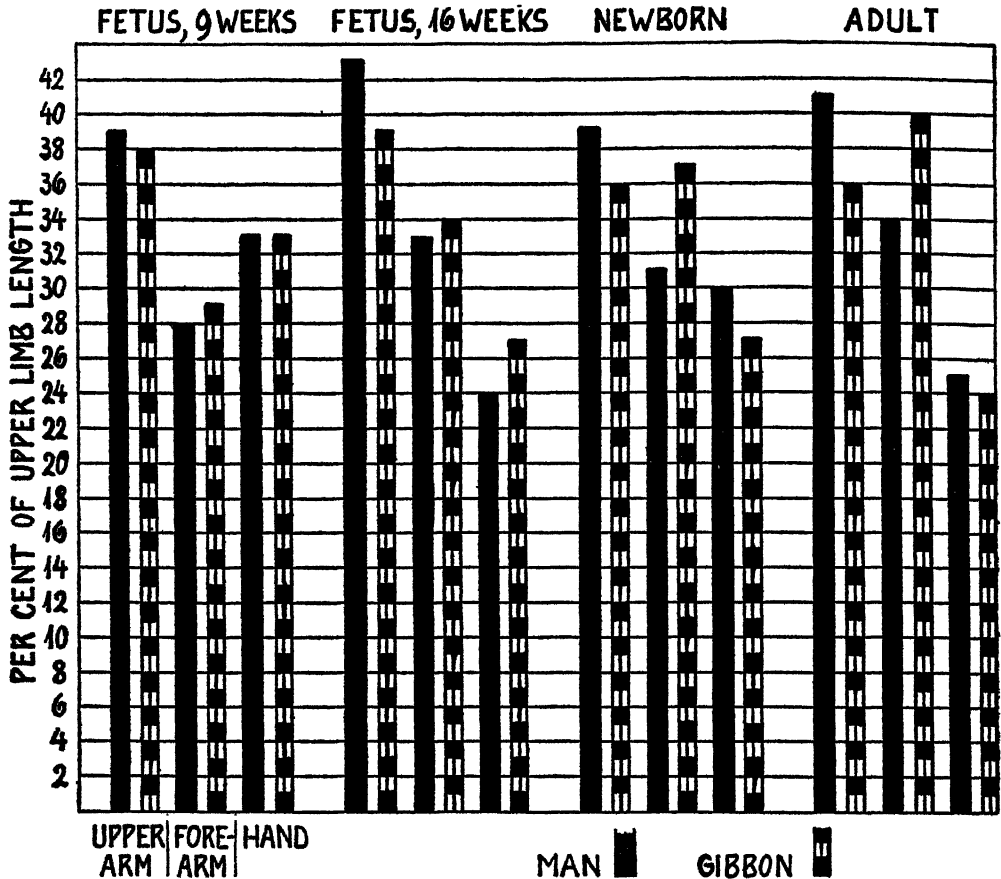


FIG. 4. DIAGRAM OF THE GROWTH CHANGES IN THE PROPORTIONS OF THE UPPER LIMB OF MAN AND OF GIBBON. The perpendicular rods represent the lengths of the upper arm, forearm, and hand in percentage of the total upper limb length. The values for man are averages from large series of whites. The values for gibbon are those of a *Hylobates concolor* (sitting height 21.5 mm.) corresponding in development to a human fetus of 9 weeks, and for the older growth stages of *Hylobates pileatus*, i.e., of a fetus (83 mm. sitting height) corresponding to a 16 weeks old human fetus, of a newborn (198 mm. sitting height), and of the averages of six adults.

lanugo can be made out of the upper arm (particularly near the elbow), while no hair at all can be detected on the lower limbs of the same specimens. In slightly older fetuses, in which the lanugo on the thighs has just become visible, the arms

toes these phalanges have either no trace of ossification as yet or only for the second and third toes.

Since the more cephalic parts of the body have a higher initial rate of growth than the more caudal parts, it can be con-

cluded that the latter must subsequently grow at a higher rate in order ultimately to catch up, so to speak, with the former. This could be shown on many examples, but it suffices to mention a few: The lower width of the trunk (hip breadth) in white fetuses forms at 9 weeks only 58 percent of the upper width (shoulder breadth), however, from the 3rd to 6th month the former grows very much faster than the latter (see tables 2 and 4), raising the proportion between the two measurements to 83 at the 24th week. In young fetuses the cervical region of the spine is

This is clearly shown by the age changes in the relation between chest circumference and trunk height, listed in table 3. In human fetuses of the 9th week this percentage proportion averages 238, in adult man only 170. In other primates the values for young fetuses are also higher than those for adults. In the orang-utan and in the howler monkey the figures indicate a tendency for a late secondary increase in this proportion, however, the individual variability in the relative chest girth is so marked in all primates that data on many more speci-

TABLE 3

Growth changes in the proportion: Chest circumference in percentage of anterior trunk height. The indices for man are approximate means, those for other primates are based upon single specimens. The development (but not the actual age) of the different monkey fetuses in a given perpendicular column corresponds approximately to that of human fetuses of the stated age in the particular column

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th-5th	6th-8th	9th-10th	Infant	Juvenile	Adult
Man (Whites).....	223.0	216.0	197.0	184.0	179.0	173.0	170.0
Orang-utan.....		213.1	208.6	208.2	197.3	209.2	209.5
Gibbon.....	198.3	199.4	180.6	173.4	168.6	167.9	148.0
Baboon.....		155.2	144.7	143.0	143.0	142.6	140.2
Macaque.....			156.6	141.9	129.2	110.3	104.5
Proboscis monkey.....		140.5	136.6	123.2			97.8
Colobus monkey.....		144.0	137.5	124.7		98.7	90.7
Capuchin monkey.....		144.6	150.4	135.3	131.7	127.4	129.5
Spider monkey.....			190.1	170.2	165.0	140.4	122.4
Howler monkey.....	175.8	176.4	162.5	152.2	142.8	141.2	149.2

more developed than the lumbar region, the former constituting 26 percent of the praesacral spine length, the latter only 25 percent. In the course of growth the relative length of the lumbar region soon surpasses that of the cervical region, which in adults has decreased to 22 percent, while the lumbar region has become lengthened to 32 percent.

IV. TRUNK

Chest circumference

The trunk becomes in general more and more slender with advancing growth.

mens are required to render this conclusion final. Should it prove to be correct, it would correspond closely to the slight secondary increase in the relative chest circumference of man between the ages of puberty and about 40 to 50 years. It is interesting to note that the amount of ontogenetic change in the relative stoutness of the trunk is very different in different primates. For instance, in the spider monkey the index drops between the fetal age of 6 to 8 months and adult life for 68 units, while in man, in the same interval, for only 27 units, and in

the baboon for only 5 units. Of special significance is the fact that the range (difference between minimum and maximum, table 3) of this index among primates of corresponding development becomes steadily larger with advance in growth. Thus, the range among fetuses of 6 to 8 months amounts to 72 units, or 43 percent of the average index in that column; in fetuses, 9 to 10 months old,

TABLE 4

Averages of the proportion: Hip breadth in percentage of shoulder breadth in white and negro fetuses and adults

AGE	WHITE	NEGRO	AGE	WHITE	NEGROES
9 weeks	58.2		26 weeks	80.5	81.5
10 weeks	62.4		27 weeks	78.5	75.4
11 weeks	63.4	64.8	28 weeks	81.7	80.8
12 weeks	68.0	64.6	29 weeks	78.3	75.3
13 weeks	69.8	66.4	30 weeks	79.2	75.8
14 weeks	74.3	69.2	31 weeks	80.5	82.7
15 weeks	74.9	76.5	32 weeks	83.9	79.1
16 weeks	78.2	76.0	33 weeks	84.8	79.3
17 weeks	79.2	77.5	34 weeks	86.6	82.8
18 weeks	80.5	80.3	35 weeks	87.1	78.9
19 weeks	80.2	78.9	36 weeks	85.8	79.3
20 weeks	79.4	77.1	37 weeks	83.3	84.4
21 weeks	82.1	81.6	38 weeks	88.2	77.7
22 weeks	82.4	78.3	39 weeks	82.0	82.9
23 weeks	81.8	83.3	40 weeks	84.0	80.5
24 weeks	83.3	82.4	Adults	90.9	86.7
25 weeks	84.0	82.0			

it is 85 units (= 55 percent of average); in juvenile primates the range amounts to 110 units (= 75 percent), and in adults to 119 units (= 87 percent). It can be stated, therefore, that even in fairly old primate fetuses the divergent specializations in the trunk shape have as yet advanced only about one half as much (relative difference between extremes 43 percent) as in adult primates (extremes 87 percent apart).

Hip breadth

With advance in growth the human trunk becomes relatively broader at its

lower end, i.e., the hip breadth increases faster than the trunk height, a conclusion which is also reached from a comparison between the increments in these two measurements, as listed in table 2. In white fetuses of the 9th week this relative hip breadth (hip breadth in percentage of trunk height) averages 42.3, at the end of the 4th month it has increased to 53.3, from then to birth it remains in general stationary, only to increase a second time during growth after birth, reaching an average of 61.5 in adult white men. This important and very marked age change escaped entirely the attention of Retzius (1904), who expressed the pelvic width in relation to body length, concluding that no changes in this proportion occur during fetal life. Weissenberg (1911) also formed an index of the hip breadth and stature in a small series of fetuses and finds it to decrease with advancing age. These two examples show again how misleading it can be to use stature as a standard in the study of growth. The conclusions of these authors are explained by the fact that any proportional increase in the width between the hips is, especially in early development, neutralized or even surpassed by the rapid increase in length of the lower extremity which forms part of the stature. Friedenthal (1914), who figured the relative hip breadth in the same way as the writer, finds it to increase during the first part of fetal growth, which is in strict agreement with the result of the author.

A few examples will suffice to show that, as in the last proportion so in this one, not only occur the age changes in various primates in a very similar way but the differences in this index between man and apes or monkeys are again much smaller in fetuses than in adults. In a gibbon fetus (*Hylobates concolor*, 56 mm. sitting height) the relative hip breadth

amounted to 39.0, in an adult of the same species to 48.8, that is a difference from the human conditions at corresponding stages of growth of 5.3 index units in case of the fetus and of 12.7 in the adult. In a howler monkey fetus (*Alouatta palliata*, 48 mm. sitting height) this proportion is 30.6, and in a full-grown specimen 43.2; the former value lies 11.1 units below that of a human fetus of corresponding development, the latter 18.3 units below that of adult man.

The relation between the upper and the lower width of the trunk is of considerable anthropological interest and this not only on account of the marked growth changes in this proportion but also for its clear racial difference. According to table 4 the two breadth diameters of the trunk approach one another more and more with advancing age. Similar ontogenetic changes occur in other primates besides man (see figure 5), e.g., the index amounts to 66.8 in a gibbon fetus (56 mm. sitting height) and to 71.8 in an adult of the same species (*Hylobates concolor*); in a macaque (*Pithecus rhesus*) it is 77.3 in a fetus (167 mm. sitting height) and 119.6 in an adult; in a howler monkey (*Alouatta palliata*) it amounts to 55.4 in a fetus (48 mm. sitting height) and to 109.2 in an adult. This index among primates seems to be correlated to a certain extent with their particular modes of progression. In those forms which are entirely quadruped, walking on all four limbs either on the ground, like the baboons, or on top of branches, like the howler monkey, the shoulder breadth is comparatively little developed, being less than the pelvic breadth in the adult. On the other hand, in primates which chiefly hang by their arms, like the gibbon, the orang, and the spider monkey, the shoulder width is relatively broad and thus retains its fetal relation to the pelvic width more closely than in the first group. The percentage

relation between hip breadth and shoulder breadth of adults amounts in the first group of primates always to more than 100, namely to 119.4 in a baboon (*Papio hamadryas*), 119.6 in a macaque (*Pithecus rhesus*), 109.2 in a howler monkey (*Alouatta palliata*), and in marmosets and lemurs, which also do not habitually hang from branches, to 113.0 in a *Saimiri sciureus*, to 104.6 in a *Seniocebus bicolor*, to 101.0 in a *Leontocebus geoffroyi*, to 117.6 in a *Callithrix penicillata*, and to 126.6 in a *Lemur variegatus*. In the second group—the forms specialized for swinging by their arms—the index is always considerably less than 100, namely 78.7 in an orang-utan, 71.8 in a gibbon (*Hylobates concolor*), 70.9 in another gibbon (*Hylobates lar*), and 92.4 in a spider monkey (*Ateles geoffroyi*).

Man, with a use of his limbs different from that of any other primate, stands in regard to this index between the extremes of the two groups discussed (gibbon 71, man 87–91, baboon 119). Again it should be mentioned that fetuses are less different in this respect than adults. For instance, at stages of development, corresponding to the end of the 5th fetal month in man, the index is in a gibbon 70.0, in man about 80, and in a baboon 90.2; i.e., a difference between the extremes of 20 units in the middle of prenatal life as compared with 48 units at completion of growth.

The human racial difference in this proportion is quite marked in the adults (see also Martin, 1914), negroes having relatively narrower hips than whites. This difference is already clearly indicated in fetal life, since the higher averages are found in whites in 23 out of the 30 week groups, for which fetuses of both races could be examined. The figures for adults in table 4 are averages for series of males. In women the index is in most, if not all, races higher than in

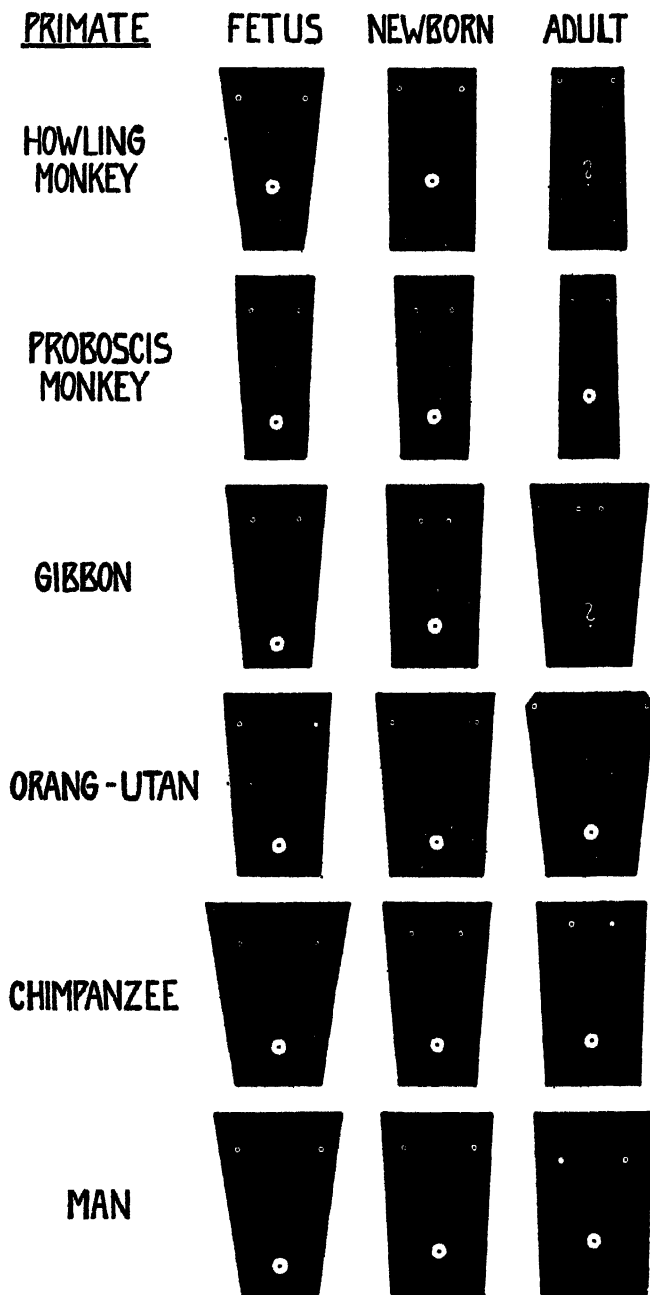


FIG. 5. DIAGRAMMATIC REPRESENTATION OF THE GROWTH CHANGES IN THE TRUNK OF VARIOUS PRIMATES

The diagrams are constructed from the anterior trunk height (drawn to equal the same size in all figures), the shoulder breadth, and the hip breadth. The exact position of the nipples of the umbilicus is shown in the figures. The fetuses of man, gibbon, and howler monkey are approximately of the same stage of development (3rd month in man), those of the other primates are somewhat older (roughly corresponding to the 5th month in man).

men, a difference which, like nearly all secondary sex differences, does not become very marked until rather late in postnatal growth.

Nipples

The diagrams in figure 5 show that during growth the nipples shift their relative position on the anterior trunk wall in a cranial direction in all the primates, except man. In the latter the nipples move in a caudal direction on the trunk during the 3rd, 4th, and 5th fetal months, from then to birth there prevails a tendency toward a relatively higher position, to change back to a secondary and marked downward migration of the nipples during postnatal growth. In relation to the ribs the human nipples change ontogenetically in the same sense, since in young fetuses they overlie the second intercostal space, and in adults they have reached the fourth or fifth ribs. The percentage relation between the distance from the level of the nipples to the upper edge of the symphysis pubis and the anterior trunk height expresses accurately the relative position of the nipples. This index amounts to about 71 in adult negroes and to about 74 in adult whites. In all other adult primates the values are higher (see also Mollison, 1911). In individual cases there may be but little difference, particularly among the macaques and baboons (e.g., one ♀ ad. *Pithecus speciosus* 74.5, one ♂ ad. *Papio hamadryas* 76.8, and one ♀ ad. *Pithecus nemestrinus* 78.7), but the great majority of monkeys and apes have very much higher indices than man, indeed, in some the nipples lie close to the supra-sternal notch or right in the axillae. Such extremely high nipples are found particularly in orang-utan (ad. ♂ 93.4), in the howler monkeys (ad. ♂ *Alouatta palliata* 97.8, ad. ♀ *A. seniculus* 99.6),

in spider monkeys (ad. ♂ *Ateles geoffroyi* 92.6, ad. ♂ *A. neglectus* 92.7), and among marmosets (ad. ♀ *Callithrix penicillata* 92.9). From these notes it can be concluded that, whereas man has the lowest placed nipples of all adult primates, this human distinction does not come about until late in growth, since in fetuses the nipples of monkeys are relatively lower, and those of man relatively higher, situated than in the respective adults. Furthermore, it seems justifiable to assume that the extreme positions of the nipples among primates are most likely late phylogenetic specializations, as they are late ontogenetic acquisitions. An orang-utan fetus (145 mm. sitting height) has an index for the relative position of the nipples of 84.9; human fetuses of the same stage of development (5th month) have an average index of 76.6 (negroes) but vary individually to a maximum of 85.9. During later growth the changes in this index diverge rapidly, causing it to rise to 93.4 in adult orang and to drop to 71 in adult negroes.

Umbilicus

In a great many adult monkeys there is absolutely no trace of an umbilical scar left and even in some juvenile primates can the umbilicus not be found. This complete absence of any umbilical scar has also been noted on other mammals (Levadoux, 1907). In all primates the umbilicus shifts in the course of growth to a relatively higher position on the trunk, as shown by the examples in figure 5, indicating a greater rate of growth in the lower than in the upper part of the trunk. This is further demonstrated by the first column of figures in table 5. These figures express the distance from the center of the umbilical cord or scar to the upper edge of the symphysis pubis in percentage of the

anterior trunk height. The relative position of the umbilicus is closely correlated to the relative length of the lumbar region of the spine, i.e., the shorter the latter the relatively lower lies the umbilicus and *vice versa*. This is true in regard to different primates as well as to the changes during growth (see table 5), and Soularue (1899) pointed out that even the slightly higher position of the

character are most likely due to the above mentioned law of cephalocaudal growth, and have no particular phylogenetic significance besides the fact that their remarkable uniformity in all primates (of which only a few examples can be listed in table 5) speaks for their close relationship.

Chest shape

The transverse and the sagittal diameter of the chest are of special interest in their relation to one another. The latter is expressed in the chest index, which indicates the general shape of a horizontal section through the thoracic region of the trunk at the level of the sternal attachment of the fourth ribs. With advance in growth the human chest becomes relatively broader, i.e., the chest index increases on account of a greater rate of growth in the transverse than in the sagittal diameter. The deep and narrow chest of the human embryo has been described by Müller (1906) and by Rodes (1906). According to the latter author human embryos and young fetuses have chest indices of 55.1, 66.6, 77.9, and 105.2 respectively at 4, 5½, 7, and 10 weeks of age. These figures were obtained from measurements taken at the level of the lower end of the sternum, but Rodes states that the proportion between these diameters differs but little from that between measurements higher up on the thorax. The writer found the chest index to change during growth from an average of 104.6 at 9 weeks of fetal life to 118.4 at 12 weeks, to remain in general the same from then to birth, and to increase again during postnatal life to at least 130.5 in white men of about 25 years.

Immediately after birth, i.e., with the beginning of breathing, the chest index undergoes according to Scammon and Rucker (1921) a sudden drop, which is

TABLE 5

*Correlation between the relative position of the umbilicus and the relative length of the lumbar portion of the spine (in percentage of the praesacral spine length) during growth and in different primates. Figures marked * calculated from data given by Mollison (1911), those marked † after Keith (1903)*

PRIMATE	AGE	RELATIVE POSITION OF UMBILICUS	RELATIVE LENGTH OF LUMBAR REGION
Orang-utan.....	Fetus	17.3	22
	Infant	18.0	23
	Adult	21.2*	24†
Chimpanzee.....	Infant	22.3	24
	Adult	25.9*	27†
Gorilla.....	Adult	27.0*	29†
Man.....	Fetus	18.5	25
	Infant	26.1	27†
	Adult	28.2*	32†
Gibbon.....	Fetus	21.4	23
	Infant	23.3	28
	Adult	30.0*	32†
Macaque.....	Adult	35.0*	42†

umbilicus in women than in men is connected with a relatively longer lumbar spine in the former than in the latter. Among adult primates the anthropoid apes have the lowest placed umbilicus, man comes next in this respect, then the gibbons, while in the large majority of the monkeys and, particularly, the lemurs the umbilicus is situated much higher on the trunk (Mollison, 1911). The developmental changes in this bodily

apparently not recovered until some weeks after birth. The indices given by these authors are, when figured in the way used in this paper, 116.2 at birth, 94.3 15 minutes after birth, 98.0 12 hours after birth, and 99.5 at the 10th day.

As shown by table 6, the growth changes in the chest index are principally the same as in man in the orang and gibbon (and probably also in chimpanzee and gorilla, for which, however, no sufficient data are available as yet). On the other hand, in the great majority of the lower primates the chest shape changes with age in just the opposite way, i.e., it

a quadruped form in which the thorax was suspended beneath the spine. The human chest shape unquestionably resembles that of adult quadrupeds much more in fetal than in adult life, as is clearly shown by the examples in figure 6. However, in very young dog fetuses the chest diameters are still the same in the transverse as in the sagittal direction, so that, in order to be consistent, one would have to make the absurd assumption that the ancestors of the dog had an upright posture. The chest shape in early embryonic life can not be regarded as the ontogenetic re-appearance of some phylo-

TABLE 6

Growth changes in the proportion: Transverse chest diameter in percentage of sagittal chest diameter. The indices for man are approximate means, those for other primates are based upon single specimens or, where two numbers are given, they represent the range of variation of two or more specimens

PRIMATE	Prenatal (month)				Postnatal		
	3rd	4th-5th	6th-8th	9th-10th	Infant	Juvenile	Adult
Man (Whites)	110 0	117 0	117 0	118 5			130 5
Orang-utan		111 5	110 0-112 0	115 2	115 5-123.4	132 2-135 4	155.6
Gibbon	98 4-112 6	113 3-117 3	106 0-114 2	115 3-123 0	117 8-115 7	115.5-117 8	129.4
Baboon		95 9	94 6-97 5	87.6-92 7	86.9-89 4	80 8-85 6	84 4
Macaque		101 3	93 0-96 0	90 7	89 2-90 0	89 2-92.1	81.8-90 3
Colobus monkey . . .		104 3	96 8-106 6	103 2		89.8	90 4
Capuchin monkey . .		96 4	95 9		92 9	90 0-92.9	88 2- 93 3
Howler monkey . . .	100 0-109.3	106 3-108 2	102 5-102 9	97 0-106 4	95 4-102.3	92.1-100 0	78 1-100 0

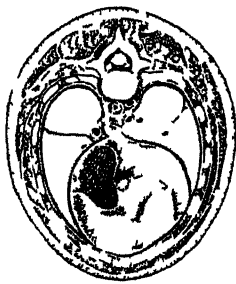
becomes steadily narrower. Thus it is found that as widely different indices of adult primates, as that of man (average 130) and of the howler monkey (individually as low as 78), have ontogenetically the same starting point, namely 110 in human fetuses of the 3rd month and as much as 109 in howler fetuses of similar development.

Some authors (e.g., Wiedersheim, 1908) familiar only with the growth changes in the human chest, have advanced the theory that the narrow and deep chest of human embryo represents a recapitulation of an ancestral condition, particularly of

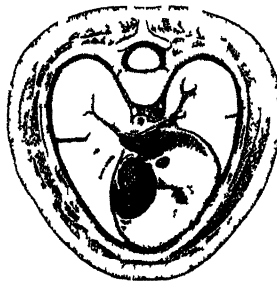
genetic condition, but is directly determined by causes of a purely topographic nature, especially by the growth of heart, lungs, and liver. After birth gravity is the most potent factor influencing the thorax shape. In quadrupeds the weight of the organs exerts a constant pressure on the sternum, thereby tending to increase the depth of the chest. In man the weight of the thoracic organs acts in a different direction, i.e., on the diaphragm. Finally, in the sloth, which habitually assumes an upright position or hangs even suspended by all four limbs, gravity affects the chest in just the opposite di-

section is in quadrupeds producing a chest index of 160 in contrast to one of about 75 in the adult dog. Table 7 demonstrates that the chest index of the sloth increases ontogenetically while that of the dog is mentioned above.

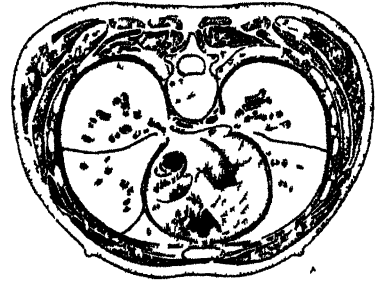
According to anthropological usage) of 88.9 in another dog from the same litter this index had decreased in adult life to 74.5. In a third dog of this litter the index remained practically constant, amounting to 86.6 in the full grown



ADULT DOG



HUMAN FETUS, 40 WEEKS



ADULT MAN

FIG. 7. CROSS SECTIONS OF THE CHEST IN AN ADULT QUADRUPED, A HUMAN FETUS AND ADULT MAN SHOWING THE PROPORTIONS BETWEEN THE TRANSVERSE AND VERTICAL DIAMETERS.

TABLE 7

Great change in the chest index of the sloth (Bathyopsis griseus). The length of the specimen is placed the length of the spine with at the tail

Age	LENGTH	CHEST INDEX
Fetus	49	102.9
Fetus	77	104.0
Fetus	90	102.5
Fetus	111	113.5
Fetus	105	114.4
Fetus	115	106.1
Fetus	130	107.1
Fetus	134	110.5
Fetus	135	110.6
Fetus	15	112
Fetus	171	115
Newborn	172	112.5
Adult ♂	465	135.4
Adult	450	132.5

decreases. By far the greatest increase occurs in the sloth during growth after birth, when gravity comes into play.

The influence of gravity on the chest shape of the dog was shown experimentally by Jackson (1907). A newborn puppy had a thoracic index (when figured

animal, and this on account of the fact that the dog had been forced to assume an upright position for 12 hours daily during one year. The author of this experiment had expected an even more marked effect of gravity on the last mentioned animal, but this seems hardly justifiable.

Height of shoulder

This discussion of the most important growth changes in the trunk would not be complete without some mention of the relative height of the shoulders. The latter is determined by the perpendicular distance between the level of the acromial point on the shoulder (see fig. 1) and that of the suprasternal notch. The greater this distance the steeper is the direction of the clavicles, on the other hand, the clavicles are horizontally posed in case the shoulders occupy one level with the suprasternal notch. From the figures in table 8 it is evident that the shoulders stand relatively higher in fetal than in

adult life of man. The most marked descent of the shoulder takes place in the white race, for which the author obtained an average index for adults of 0.1. According to Martin (1914) the acromion lies even 8 to 10 mm below the upper edge of the sternum in adult Europeans. It can be stated therefore that in adult

the higher than in the lower races. One might argue further than the height of the shoulder of the arboreal primates is directly connected with the fact that their upper limbs support part or all of the body weight and thus tend to pull or push the shoulders upward.

Table 8 shows that the orang, gibbon,

TABLE 8

Relative shoulder height (distance from middle of line connecting acromial points to suprasternal notch in percentage of anterior trunk height) during growth of whites and in adults of Senois (calculated from data given by Martin, 1905), negroes, apes and monkeys

MAN			APES AND MONKEYS			
Age	Race	Average	Age	Primate	Minimum	Maximum
3rd month	White fetus	4.0	Adult	Orang-utan	13.8	
4th month	White fetus	7.0	Adult	Gibbon	12.0	
5th month	White fetus	6.9	Adult	Baboon	3.4	5.9
6th month	White fetus	6.6	Adult	Macaque	3.9	5.1
7th month	White fetus	5.7	Adult	Colobus monkey	3.7	4.6
8th month	White fetus	4.7	Adult	Proboscis monkey	7.9	
9th month	White fetus	4.8	Adult	Guenon monkey	4.8	9.0
10th month	White fetus	3.6	Adult	Patas monkey	3.8	4.1
Adult	White male	0.1	Adult	Capuchin monkey	4.6	10.0
Adult	Senoi male	2.7	Adult	Spider monkey	8.3	13.6
Adult	Negro male	3.0	Adult	Howler monkey	12.1	14.2

whites in a normal position of rest the clavicles are either horizontally posed or point even downward with their lateral ends. In fetuses the clavicles diverge upward, deviating from a horizontal position in individual cases for as large an angle as 32° (see fig. 7). The adult Senois, negroes, and, judging by photographs alone, many other lower races remain in regard to the relative position of the shoulder closer to the fetal condition than whites. In adult apes and monkeys the shoulders are always situated relatively high (see table 8) and undergo practically no change during growth. It seems safe to conclude from these notes that the descent of the shoulders in man represents a comparatively new evolutionary experiment among primates, which has progressed farther in

and spider monkey, which swing by their arms, have actually the relatively highest



FIG. 7. WHITE FETUS OF THE 10TH WEEK SHOWING STEEPLY ASCENDING CLAVICLES (THE HEAD WAS OMITTED SINCE, IN ITS NATURAL POSITION, IT WOULD HAVE PARTLY OBSCURED THE CLAVICLES)

shoulders, while the lowest ones are found in the largely terrestrial baboons. The high indices of the howler monkeys are due to the fact that their suprasternal notch is situated abnormally low in conse-

adult life (see also Todd, 1912), the shoulder, respectively the highest point of the scapula, sinks according to Wolf (1925) from the level of the 4th cervical vertebra in a young fetus (18.5 mm.

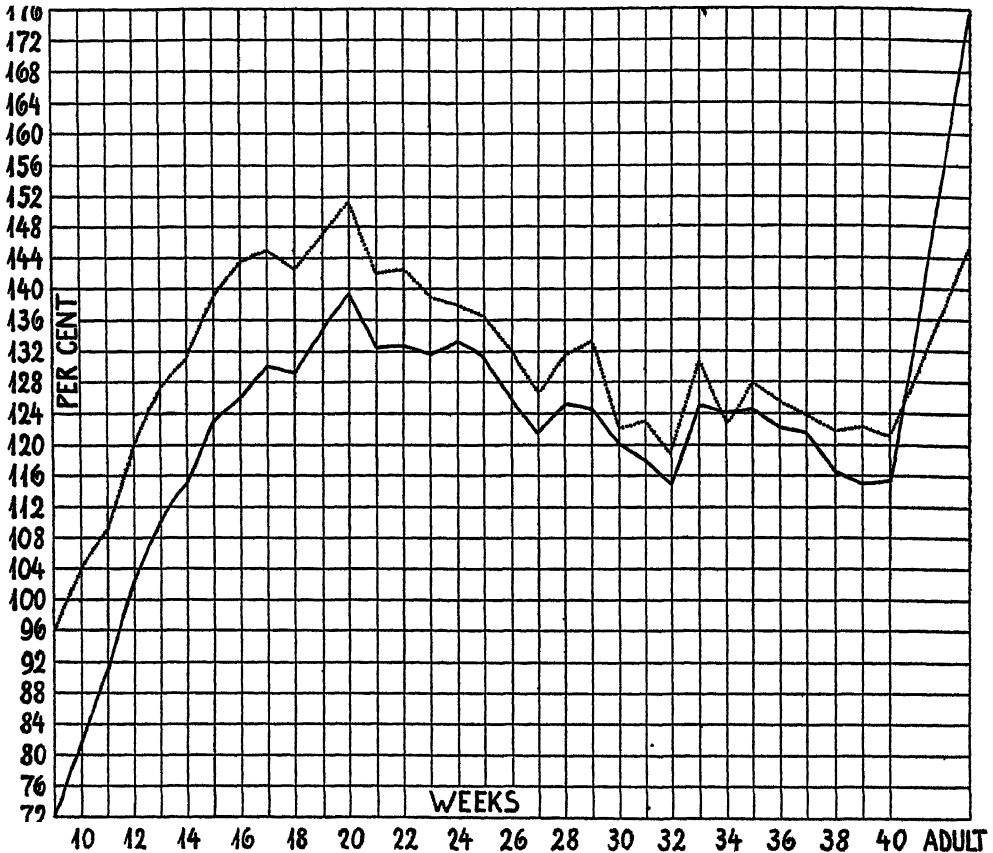


FIG. 8. CURVES OF GROWTH IN WHITE FETUSES AND ADULTS FOR THE PROPORTIONS: TOTAL LENGTH OF UPPER LIMB IN PERCENTAGE OF ANTERIOR TRUNK HEIGHT (DOTTED LINE) AND TOTAL LENGTH OF LOWER LIMB IN PERCENTAGE OF ANTERIOR TRUNK HEIGHT (SOLID LINE)

quence of the greatly enlarged hyoid capsule and of the forking in the manubrium sterni.

In relation to the spine the shoulders descend during human growth even more markedly than in relation to the upper edge of the sternum. While the latter moves only from the level of the seventh cervical vertebra in early fetal life to that of the second thoracic vertebra in

sitting height) to that of the fourth thoracic vertebra in adults.

V. LIMBS

Total lengths of limbs in relation to trunk height

The relation in length between the extremities and the trunk changes very markedly in the course of growth. As

shown by the curves in figure 8, at 9 weeks of human fetal life both the upper and the lower limbs are still shorter than the trunk, but the latter increases at a slower rate than the former so that, at the end of the 5th month, the extremities greatly exceed the trunk in length. From then to birth the limbs grow more slowly than the stem, causing the relative limb lengths to decrease somewhat irregularly. During postnatal growth the limbs show

TABLE 9

Averages in white and negro fetuses and adults for the proportion: Total length of upper extremity in percentage of total length of lower extremity

AGE	WHITES	NEGROES	AGE	WHITES	NEGROES
9 weeks	132.7		26 weeks	104.8	109.2
10 weeks	126.8		27 weeks	104.2	108.1
11 weeks	119.8	123.1	28 weeks	105.3	107.4
12 weeks	116.6	121.3	29 weeks	106.8	106.7
13 weeks	115.8	118.3	30 weeks	101.4	102.9
14 weeks	114.1	114.7	31 weeks	104.5	105.5
15 weeks	112.8	116.1	32 weeks	103.4	107.1
16 weeks	113.2	113.9	33 weeks	104.5	104.5
17 weeks	111.6	113.2	34 weeks	99.3	104.5
18 weeks	110.5	112.2	35 weeks	103.6	106.5
19 weeks	108.7	109.1	36 weeks	103.3	106.6
20 weeks	108.2	109.7	37 weeks	102.1	104.6
21 weeks	107.4	112.7	38 weeks	104.9	106.7
22 weeks	107.0	107.6	39 weeks	105.9	104.4
23 weeks	105.6	108.0	40 weeks	104.9	102.7
24 weeks	103.8	106.4	Adults	82.5	83.4
25 weeks	104.2	105.4			

again a greater growth rate than does the trunk, since the curves ascend a second time. These findings for fetal growth agree in principle with the results obtained by Reicher (1923), those for postnatal growth are in accord with the studies by Schwerz (1910), Weissenberg (1911), and others.

Relation in length between upper and lower limb

At the beginning of fetal development the arm length is very much greater

(about one third) than the length of the lower limb, but with advancing age the two curves in figure 8 approach one another more and more until, soon after birth, they cross, when the leg becomes longer than the arm. This direct relation between the lengths of the upper and lower limb is clearly expressed in the so-called intermembral index, which is listed in table 9. This index decreases from the 3rd to the 6th month of fetal life, remains about constant from then to birth, to drop again in postnatal life. In general these growth changes bear out those obtained by Retzius (1904), Weissenberg (1911), and Reicher (1923); the actual sizes of the indices are somewhat at variance, mostly on account of differences in the method of measuring and calculating the proportion. The figures in table 9 permit the conclusion that negroes have somewhat longer upper limbs, in proportion to the lower ones, than whites and this not only at completion of growth but already in fetal life. The only apparent exception to this—immediately before birth—can not be regarded as very significant, since those averages are based upon small series of specimens only. In regard to this particular proportion the negro has gone not quite as far in a peculiarly human specialization as the white. Relatively long arms and short legs, resulting in a high intermembral index, are decidedly simian characters, whereas the reversed relation is typical for man, the only primate in which the index drops considerably below 100 in adult life. These facts are demonstrated by a comparison of tables 9 and 10. It is very noteworthy that this index undergoes a much more profound ontogenetic change in man (a decrease of about 50 units) than in any other primate; in the gibbon, e.g., it decreases for not more than 20 units and in the howler

monkey about 26 units. The tremendous difference in this proportion between various adult primates is not yet nearly as marked in fetal stages of development. For instance, in the adult gibbon the intermembral index amounts to as much as 159.1, which is 77 units above the value for adult white man; on the other hand, in a gibbon fetus, corresponding to a human fetus of the 3rd month, the index is as low as 157.6, which surpasses the average for 3 months old white fetuses by only 34 units.

The differences in the relative lengths of the limbs among adults of the higher

230.8; *H. agilis* 232.3; *H. concolor* 280.0). In monkeys this relative upper limb length is, as a rule, markedly shorter than in man, except in such highly specialized forms as the spider monkeys (*Ateles geoffroyi* 176.1, 207.0, and 244.5; *A. paniscus* 187.8; *A. neglectus* 235.5) and some woolly monkeys (*Lagothrix infumata* 167.1). During individual development these different specializations in man and anthropoid apes make their appearance at quite different periods. As shown in the frontispiece, the extreme arm length of apes is already well defined in early fetal life; on the other hand, the unequalled length of the lower

TABLE 10

Growth changes in apes and monkeys in the proportion: Total length of upper extremity in percentage of total length of lower extremity. The figures for gorilla and some of those for chimpanzees have been obtained from data in the literature. The fetuses in a perpendicular column correspond in their development approximately to human fetuses of the age stated at the top of the particular column

PRIMATE	AGE					
	Prenatal (month)			Postnatal		
	3rd	4th-6th	7th-10th	Infant	Juvenile	Adult
Gorilla.....		155.8				146.7
Chimpanzee.....		147.7	138.1	147.7-137.9	145.5	149.3-136.3
Orang-utan.....		181.1	174.3-171.7	178.9-172.1	175.2-170.1	166.7
Gibbon.....	173.4-157.6	157.8-155.8	161.2-156.3	155.6-150.3	165.0-150.7	159.1-153.5
Baboon.....		136.8-128.1	128.1-127.4	126.6	114.7-110.4	113.6-113.3
Macaque.....		131.8	127.2-126.2	126.4-124.4	122.9-114.6	119.2-107.8
Capuchin monkey.....		128.0	130.5	120.5	114.7-108.2	106.3-104.3
Howler monkey.....	149.2-146.0	144.5-136.4	138.1-137.3	139.5-133.3	130.7-124.8	130.6-122.7

primates are at once apparent in the diagrams of the frontispiece to this paper. Whereas in the apes the upper limbs are greatly lengthened, in man it is the lower limb which shows, indeed, a unique development. In relation to the trunk height the total length of the lower extremity is far greater in adult man than in any other adult primates. In regard to his relative upper limb length adult man occupies an intermediate and conservative position. This latter proportion amounts on a rough average to 145 in man, to 188 in gorilla (Mollison, 1911), and to 248 in the gibbon (*Hylobates lar*

limb, characteristic of adult man, is not yet even indicated in intrauterine life, several of the ape fetuses surpassing the human fetus in this respect. Even at birth man has still proportionately short lower extremities, namely in percentage of the trunk height on an average in whites 115.7, as compared with 175.4 in white adults. In this, man resembles very closely the growth changes in the jumping mouse, in which the posterior limbs have also become greatly lengthened. In newborn jumping mice, just as in the human baby, this extreme condition is not yet apparent (Tschulok, 1922).

It is not to be doubted that the ancestors of these specialized rodents once possessed shorter posterior limbs, and that, therefore, their ontogeny repeats their phylogeny in this respect. To be consistent, one now has to conclude that the corresponding late growth change in man also points to relatively shorter legs in human ancestors. One is tempted to argue further from the ontogenetically much later appearance of the unique human leg length than of the characteristic arm length of the apes, that the latter specialization was phylogenetically much earlier acquired than the peculiarity of man. However, this last assumption is offered merely as a suggestion, which needs support from additional investigations.

Relations in length between the proximal and middle segments of the limbs

The proportions between the length of the proximal and middle segments of the limbs undergo some changes during growth, which are shown in a condensed form by table 11. Both, the upper arm-forearm index and the thigh-leg index increase with advancing age, particularly up to the 5th fetal month and again in postnatal life. These findings, which are based upon a material of 623 fetuses, are not in agreement with the results of some other authors. Based upon a study of 22 specimens Hamy (1872) claims that the upper arm-forearm index of fetuses is higher than that of adults. The same conclusion was reached by Mendes Corrêa (1919), who had measured only 10 specimens and used the data by Serrano (1895) on 6 additional ones. According to the former author the thigh-leg index also decreases with advancing age. Nishizuka (1925) found no uniform growth change in these proportions in Japanese; the following averages show this clearly: humero-radial index in fetuses of the 4th

month (10 specimens) 73.6, in newborns (10 specimens) 74.1, in children (5 individuals) 69.1, and in adults (20 individuals) 71.5; femoro-tibial index at the same growth stages 74.7, 76.3, 76.4, and 75.9 respectively. Reicher's (1925) investigations on over 500 white fetuses revealed the following growth changes: The upper arm-forearm index rises from 76 at 9 weeks of fetal life to 79 at 10 weeks, during the 4th month it drops to 78, but rises again to 81 in the 5th month, fluctuating from then to birth between

TABLE 11
Upper arm-forearm and thigh-leg proportion in white and negro fetuses and adults

AGE	$\frac{\text{FOREARM}}{\text{UPPER ARM}} \times 100$		$\frac{\text{LEG}}{\text{THIGH}} \times 100$	
	Whites	Negrees	Whites	Negrees
3 months, 1st half.....	72.9		66.7	
3 months, 2nd half.....	73.6	73.6	69.2	69.3
4 months.....	74.6	75.8	75.5	75.7
5 months.....	77.7	78.9	79.9	80.8
6 months.....	77.9	79.4	81.3	81.9
7 months.....	78.0	79.5	80.9	82.6
8 months.....	78.0	81.2	79.0	81.3
9 months.....	79.2	81.9	79.0	82.2
10 months.....	79.2	80.5	79.0	80.5
Adult males.....	83.6	91.4	84.1	84.9

the averages of 80 and 81.5. The thigh-leg index increases from 78.5 in the 9th week to 85.5 in the 5th month, afterwards the averages decrease again to 84.5 in the 7th to 9th months, and to 81.5 in newborns. Even in regard to the postnatal changes in these indices no agreement has been reached as yet. For instance, Godin (1910), like the writer, finds the upper arm-forearm index to increase with age, namely, from 77 at 13 years to 83 at 17 years. Schwerz (1910), in contrast to this, obtains a

decrease from 82.6 at 7 years to 78.1 at 20 years. The discrepancies in these results can not be entirely due to differences in the material under investigation but are, undoubtedly, to be accounted for to a very considerable extent by differences in the technique employed. The particular findings of the writer in regard to the growth changes in whites agree in principle very well with those obtained for negroes and are further supported by the analogous changes in other primates, as shown by the examples in table 12.

man in this respect (humero-radial index in 2 gorilla skeletons, Hopkins collection: ad. ♂ 78.9, ad. ♀ 78.2). In a large variety of other primates the forearm exceeds the upper arm in length, for instance, in a few individual chimpanzees and orangs (Sonntag, 1924), in all gibbons, and in most baboons and spider monkeys. Inasmuch as the forearm is proportionately shorter in fetuses than in adults, and particularly since an extreme length of the forearm, surpassing that of the upper arm, is found only in late onto-

TABLE 12.

Growth changes in the upper arm-forearm and thigh-leg proportions of the gibbon and of the spider monkey. The specimens are listed according to increase in body size.

GIBBON (HYLOBATES PILEATUS)				SPIDER MONKEY (ATELES GEOFFROYI)			
Age	Sitting height	Forearm : upper arm	Leg : thigh	Age	Sitting height	Forearm : upper arm	Leg : thigh
	mm.				mm.		
Fetus	83	87.2	79.1	Fetus	178	87.0	93.9
Fetus	102	92.5	79.8	Fetus	187	89.3	93.0
Fetus	158	98.3	80.8	Newborn	191	87.7	90.6
Fetus	169	99.2	85.5	Newborn	195	88.8	90.0
Newborn	198	101.1	86.5	Infant	201	90.6	91.7
Juvenile		102.2	90.1	Infant	204	90.4	92.4
Juvenile		105.1	89.4	Infant	232	92.3	94.3
Adult		111.2	89.2	Juvenile		96.1	91.1
Adult		109.7	88.7	Juvenile		100.0	95.0
Adult		108.3	88.7	Juvenile		100.5	89.9
Adult		112.1	89.3	Adult		99.0	91.3
Adult		114.3	89.6	Adult		102.2	92.5
Adult		112.1	91.0	Adult		100.9	91.7

and by those contained in a former paper by the author (1924 b, table 4). In a pregnant rhesus monkey, received recently, the upper arm-forearm index amounted to 96.5, whereas in the fetus (sitting height 163 mm.) of this specimen to only 90.5.

Among adult primates man possesses one of the relatively shortest forearms. Some of the primitive marmosets equal the human upper arm-forearm index (*Callithrix jacchus* 82.6 and 84.8, *C. penicillata* 84.8, *Leontocebus geoffroyi* 80.5 and 84.4). Of the higher primates gorilla alone rivals

genetic stages (see table 12), it seems justifiable to assume that man and gorilla are conservative and primal in this proportion, whereas such forms as the gibbon have a highly specialized forearm.

In regard to the thigh-leg proportion, adult man is very similar to gorilla and chimpanzee, but has considerably lower values than the large majority of the lower monkeys. In some of the latter, as for instance in the spider monkey (table 12), this index does not increase with advancing growth.

It is of special interest to note that the

averages of both the indices, listed in table 11, are larger in negroes than in whites, and this in fetal as well as in adult life. This might be interpreted on the basis of the above discussion as indicating

primates have led him to disagree with the assumption of Mollison (1911) that the humero-radial and femoro-tibial indices of man have decreased in the course of evolution; he is inclined rather to the

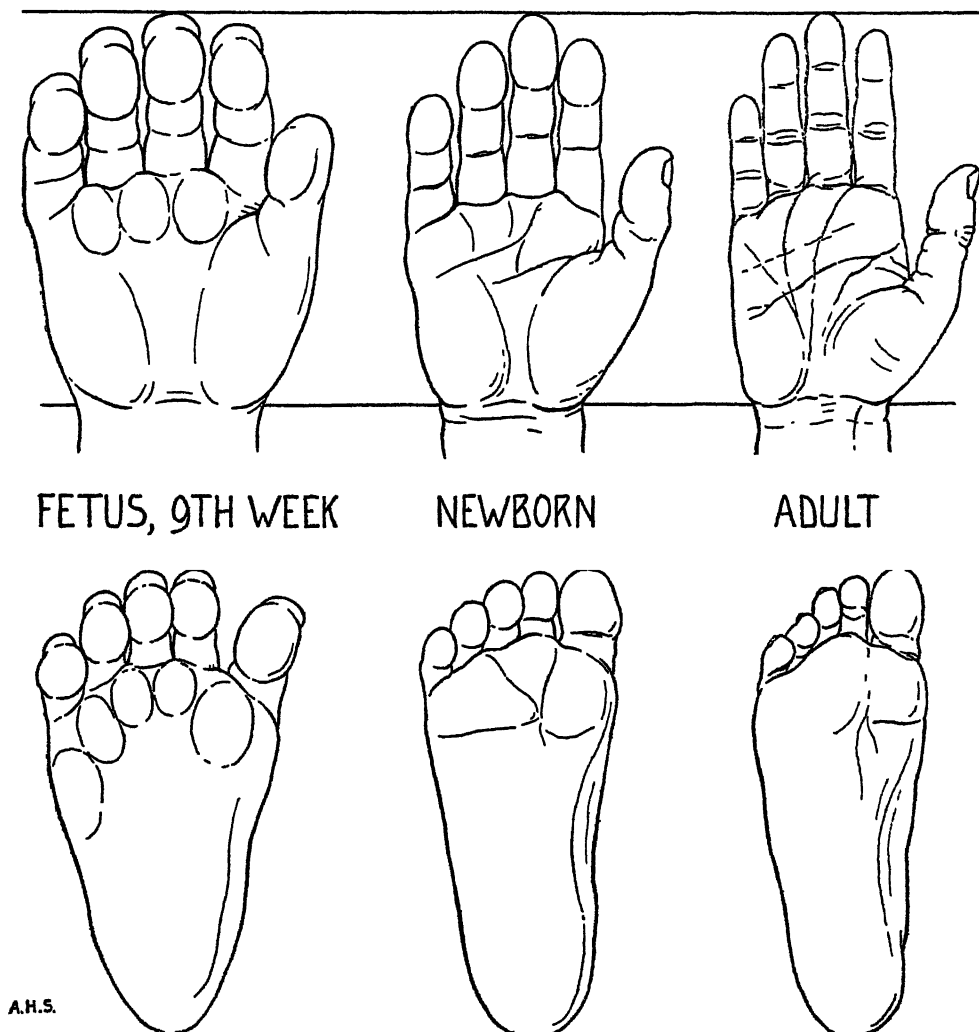


FIG. 9. DIAGRAMS ILLUSTRATING THE GROWTH CHANGES IN THE HUMAN (WHITE) HAND AND FOOT

that these particular limb proportions have phylogenetically been even less modified in the white than in the negro. In the latter race they tended slightly in the direction which is typical of monkeys. The writer's studies on the ontogeny of

belief that these proportions have, if at all, become but little altered. The only direct evidence, available so far, would certainly support the author's view, since these indices are rather low in Neanderthal man (skeleton of La Ferrassie:

humero-radial index 73.8, femoro-tibial index 76.6, Boule, 1911-13).

The racial difference in the thigh-leg index, derived from living adults, happens to be rather small. This difference was much larger in the closely corresponding femoro-tibial index, which was obtained by the author on 270 extremities from dissecting rooms. The indices of this material averaged 84.06 in white males, 85.71 in negro males, 83.88 in white females, and 86.10 in negro females.

VI. HAND AND FOOT

The most distal segments of the extremities—the hand and the foot—have

of the hand and of the foot in monkeys equals that of man at early stages of development, i.e., about the time of the separation of the digits, is demonstrated by the illustrations of Keibel (1906). The initially very high hand index becomes reduced very rapidly in the large majority of the monkeys and apes. In man this decrease proceeds more slowly and is less marked. Of all adult primates man and gorilla have the relatively broadest hands and thus retain the fetal condition much more closely than other forms do. In regard to the foot index the growth changes and the value in the adult of man fall well within the range

TABLE 13

Growth changes in primates in the proportion: Hand breadth in percentage of total hand length. The indices for man are approximate means, those for other primates are based upon single specimens or, where two numbers are given, they represent the range of variation of two or more specimens

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th-5th	6th-8th	9th-10th	Infant	Juvenile	Adult
Man (Whites).....	57.8	53.0	53.0	52.7			45.0
Orang-utan.....		34.0	37.0-37.4		31.5-36.8	29.2-38.2	22.0-28.1
Gibbon.....	34.5	29.6-37.4	29.2-31.0	29.0-32.2	23.5-32.5	24.1-26.5	21.7-25.0
Baboon.....		47.0	42.4-45.0	43.8	36.0-40.8	38.5-41.5	42.0
Macaque.....		40.8	38.7-39.3	36.5-38.5	35.7	35.0-35.9	32.0-33.3
Colobus monkey.....		41.4	38.0-38.7	35.3		31.5	29.1
Capuchin monkey.....		42.1	43.5	44.8		35.7-38.5	34.0-38.9
Howler monkey.....	42.1-42.9	39.9-45.2	39.5-40.5	38.0-39.2	36.5-37.8	32.7-36.2	31.0-33.9

undergone very marked and widely differing evolutionary changes in primates with different specializations. The ontogenetic changes in these parts are of particular interest since they are apt to throw light at least on the important problem of the primitive ancestral conditions in the original primate hand and foot.

Relative width of hand and foot

The hand as well as the foot becomes relatively narrower with advancing growth, as shown by figures 9 and 13 and by table 13. That the relative width

of variation of these conditions in other primates. Both, the hand and the foot, are relatively longer and narrower in negroes than in whites, racial differences which can be recognized even in the averages of large series of fetuses.

Fingers

The middle finger is the longest of all fingers in all the primates and at any stage of growth, with the single exception of some prosimiae, in which the fourth finger may be the longest (at least in adults). In all primates the fourth finger

extends farther than the second finger, but this rule has also its exception, though this time it is found in man. According to table 14, white fetuses of the third month have in 2 percent of the cases the index finger surpassing the ring finger in length. This frequency increases rapidly, to reach 23 percent in adult whites. In negroes this particular relation is found in only 3 percent of adults and never in fetuses. The white race has therefore progressed farther than the negro in regard to this condition which, undoubt-

TABLE 14

Percentage frequencies of the relation in length between the second and fourth finger in white and negro fetuses and adults. (<"smaller than", >"larger than")

$\Pi < IV \quad \Pi = IV \quad \Pi > IV$

3rd month.	Whites	33	65	
	Negroes	57	43	0
4th-5th month....	Whites	15	67	18
	Negroes	49	51	
6th-8th month....	Whites	17	69	14
	Negroes	51		0
9th-10th month...	Whites	32	54	14
	Negroes	59	41	0
Adults.	Whites	18	59	23
	Negroes	55	42	3

edly, represents a human peculiarity of relatively recent origin, and certainly one which at best is still very rare in early ontogenetic stages.

The relation between these two fingers in adults has been studied a good deal, most authors agreeing that a longer index finger is more frequent in women than in men, much more frequent in whites than in negroes, and among the former most frequent in jews (Ecker, 1875; Mantegazza, 1877; Grüning, 1885; Weissenberg, 1895; Féré, 1900; Daffner, 1902). Among adult male Indians the author (1926)

found a longer index finger in only 3 percent of the cases, i.e., in the same frequency as in adult male negroes.

Thumb

The thumb, when measured from the styloid process of the radius to the tip of the digit, becomes shorter in relation to the total hand length with advancing growth, and this in all primates. In man this ontogenetic decrease (see table 15 and fig. 9) is less marked than in apes or monkeys, indeed, in man (and in the baboon) there seems to prevail a tendency for a slight secondary increase in the

TABLE 15

Averages for white and negro fetuses and adults of the proportion: Length of thumb in percentage of total hand length

3rd month, 1st half..	74.0	
3rd month, 2nd half.	74.7	71.6
4th month.	72.9	69.9
5th month.	71.1	69.9
6th month.	70.4	67.2
7th month.	68.7	66.7
8th month.	67.9	66.5
9th month.	68.0	65.9
10th month.	67.7	65.8
Adult males.	69.2	66.8

relative thumb length during postnatal growth. The adult human thumb is the longest and least changed of all primate thumbs; those of gorilla, baboon, and capuchin monkey come nearest to the human thumb in relative length, while among all the other primates the thumb is either short or has even become nearly or entirely eliminated. Examples for the latter tendency are shown in figure 10. In many species of the African *Colobus* monkeys a free thumb has disappeared completely in adults; in fetuses, however, this digit is still fairly well developed (fig. 10, No. 1). Sir Harry Johnston (1904), speaking of the species *Colobus*

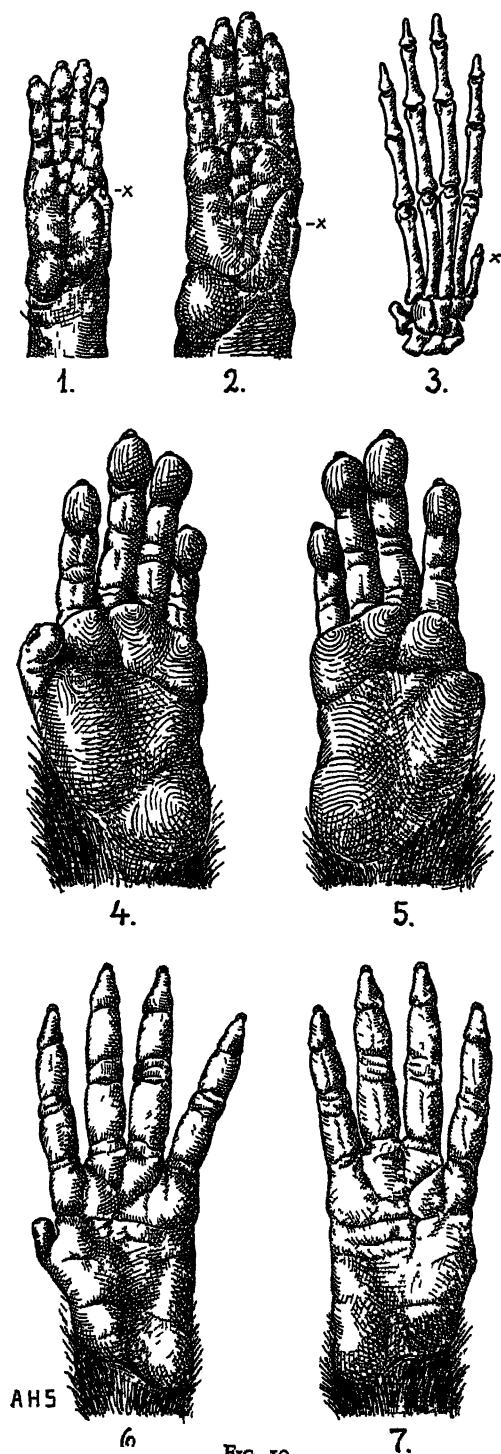


FIG. 10

tephrosceles, mentions that there is only "the minutest trace of a thumb nail in the place where the thumb is missing . . . but the young *Colobuses* of this species have a complete thumb only a little smaller than this finger would be in the *Cercopithecus*. As the animal grows to maturity, so its thumb dwindles, until in a very old male there may be absolutely no trace left of the missing finger." In all the Guenon monkeys the thumb is very small and can be of but little use. In one specimen, recently obtained by the author, the free thumb was entirely missing on one hand (fig. 10, No. 5); that this was not due to any injury is proved by the fact that there is absolutely no trace of any scar formation. This hand represents a progressive variation, foreshadowing the future fate of the Guenon hand, just as the atavistic re-appearance of a free thumb on the hand of an occasional spider monkey (fig. 10, No. 6) is the individual reversion to an ancestral condition. Among 58 spider monkeys the author found two in which the thumb was still present on one hand only.

From these notes it can be concluded that among the arboreal primates there exists a wide-spread tendency toward the elimination of the first finger—a specialization which reaches its extreme only at completion of growth and which varies

FIG. 10. EXAMPLES SHOWING THE TENDENCY AMONG PRIMATES TO REDUCE THE THUMB

Nos. 1, 2, and 3 hands of *Colobus* monkey (*Colobus abyssinicus sturicus*), rudimentary thumb at x, No. 1 fetus (112 mm. sitting height), No. 2 older fetus (134 mm. sitting height), No. 3 adult female (metacarpus and one phalanx of thumb still present but proportionately very small and not visible on outer hand). Nos. 4 and 5 left and right hand of adult male Guenon monkey (*Lasiopyga pygerythra*), left thumb of typical size for these particular monkeys, right thumb congenitally missing on the outer hand (metacarpus I present but small). Nos. 6 and 7 left and right hand of infantile female Spider monkey (*Ateles geoffroyi*); the complete lack of an outer thumb is normal for Spider monkeys, but on the left hand of this specimen the thumb is still present, containing a well developed metacarpus and two fused phalanges.

individually to a considerable extent. This evolutionary trend has not affected man, whose thumb has changed but little from the relative length, typical of all young primate fetuses.

The racial difference in this proportion, according to which the negroes have at all ages a considerably shorter thumb than whites (table 15), marks the former as slightly more "simian" in this respect, and, as it happens, the white as even more original or "primitive."

In early fetal life the free thumb branches from the palm immediately at the base of the index finger. In the course of growth this place of branching shifts proximally to a place nearer the wrist (see fig. 9). This ontogenetic migration

original primate hand. It is significant, but not surprising, therefore, to find that this condition is still lacking in the human embryo. Not only does the embryonic thumb branch at a place unfavorable for effective opposability but it is not yet rotated around its longitudinal axis to face the other digits, as is clearly shown by the diagrams in figure 11.

Toes

Among primates the middle toe reaches, as a rule, farther than any of the other toes. Exceptions to this are found among the lemurs and marmosets, in which the fourth toe often equals the third in length, or, in rarer cases, may even surpass it (e.g., in one out of 8 marmosets of the

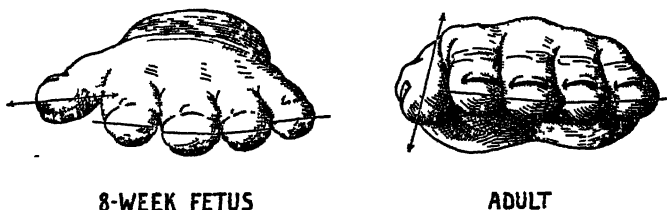


FIG. 11. FETAL AND ADULT HAND OF MAN, SEEN FROM IN FRONT, SHOWING THE ROTATION OF THE THUMB
The straight lines run parallel to the transverse axes of the finger nails

is most pronounced in orang-utan and gibbon, somewhat less in other anthropoids and man, as well as in most Old World monkeys, while in the large majority of the American monkeys no such shifting takes place at all, the thumb persisting in its typically fetal position throughout life. This movement of the thumb, away from the other fingers, in the catarrhine hand has greatly facilitated the opposability of the thumb. In platyrrhines this digit is either not opposable at all, as in the marmosets, or, as in the *Cebidae*, only to a much lesser degree than in the African and Asiatic primates. The opposability of the thumb, which was and is of greatest importance for the evolution of man, was not yet a feature of the

author's collection). The only other exception is man, in whom the second or even the first toe has become the longest. It is very interesting that early in ontogeny man still shows occasionally the typical digital formula of his simian relatives, since in 4 to 5 percent of human fetuses from the beginning of the 3rd month the middle toe is the longest (fig. 12). In very rare instances this, for man undoubtedly primitive, condition may even persist to adult life; Wood Jones (1920) mentions two such cases and Hawkes (1914) found it in 19 persons. Table 16 demonstrates the gradual changes during human growth in the relations in length between the toes. In the beginning of fetal life the great toe is never

longer than the second toe, but the reversed relation occurs in 98 percent of whites. On the other hand, in adult whites the second toe is the longest in only 12 percent of the cases, while the great toe has surpassed the others in 52 percent. The latter condition is, phylogenetically speaking, a relatively new and exclusive acquisition of man. In the white race it is found with much greater frequency than in the negro, who has remained in this point somewhat less specialized than the average white, and who certainly tends to retain the fetal condition more closely.

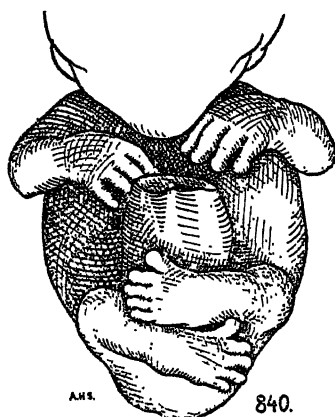


FIG. 12. FRONT VIEW OF A HUMAN FETUS (25 MM. SITTING HEIGHT) WITH MIDDLE TOE LONGER THAN THE OTHER TOES

Note also the short and abduced great toes

There exists a considerable literature on the relative length of the first two toes of adult man, a large part of it centering on a sex difference in this feature. How uncertain, however, such a sex difference must be, is evident from the conflicting results. For instance, Harrison (1884), Daffner (1902), and Hawkes (1914) find a longer second toe more frequently in women than in men, Grüning (1885) maintains just the opposite, while Weissenberg (1895) claims that there is no difference in the two sexes. According

to Maurel (1888) the second toe surpasses the first in length more frequently in Mongolian races than in whites or negroes.

In man the distance from the heel to the tip of the great toe increases with advance in growth faster than the foot length, measured to the tip of the middle toe. This relation is just the opposite in monkeys and apes, i.e., the great toe becomes relatively shorter. This is illustrated by figure 10 and, especially, by figure 13. The latter figure also shows

TABLE 16

Percentage frequencies of the different relations in length between the first three toes in white and negro fetuses and adults

AGE	RACE	DIGITAL FORMULA				
		I △ II △ III	I △ II II III	I △ II V III	I II III V III	I V II V III
3rd month.....	White	4	6	88	2	0
	Negro	5	5	95	0	0
4th-5th month..	White	0	0	40	44	16
	Negro	0	2	81	12	5
6th-8th month..	White	0	0	28	34	38
	Negro	0	0	43	42	15
9th-10th month..	White	0	0	11	31	58
	Negro	0	0	39	38	23
Adults.....	White	0	0	12	36	52
	Negro	0	0	39	40	21

that the phalangeal portions of the lateral toes (II to V) are, in regard to their relative lengths, little different in the fetuses of man and monkey. But, while these digits have become relatively shorter in adult man, they have increased their proportionate length tremendously in the adult monkey. This leads to the conclusion that even such widely different types of feet as those of man, with their extremely short lateral toes, and those of the howler monkey, in which these toes

are excessively developed, can ontogenetically be traced to very similar forms, from which the different specializations cause them to grow in opposite ways, whereby the monkey foot changes more profoundly than the human foot.

Gorilla may be an exception to the rule stated above that the great toe becomes relatively shorter in monkeys and apes, but the different species of this ape vary considerably in this respect. The following values for the relative length of

Akeley, donated by Amer. Museum of Natural History) 91.6; adult (Hartmann, 1880) 85.1.

For chimpanzee the following figures are available: newborn (preserved specimen, lent by Dr. Huntington) 86.3; infant (preserved specimen, lent by U. S. National Museum) 85.1; adult (Beddard, 1893) 74.2; several other adults (from various photographs) 78-85; adult male (cast by C. H. Ward) 89.5.

In orang-utan the index was found to

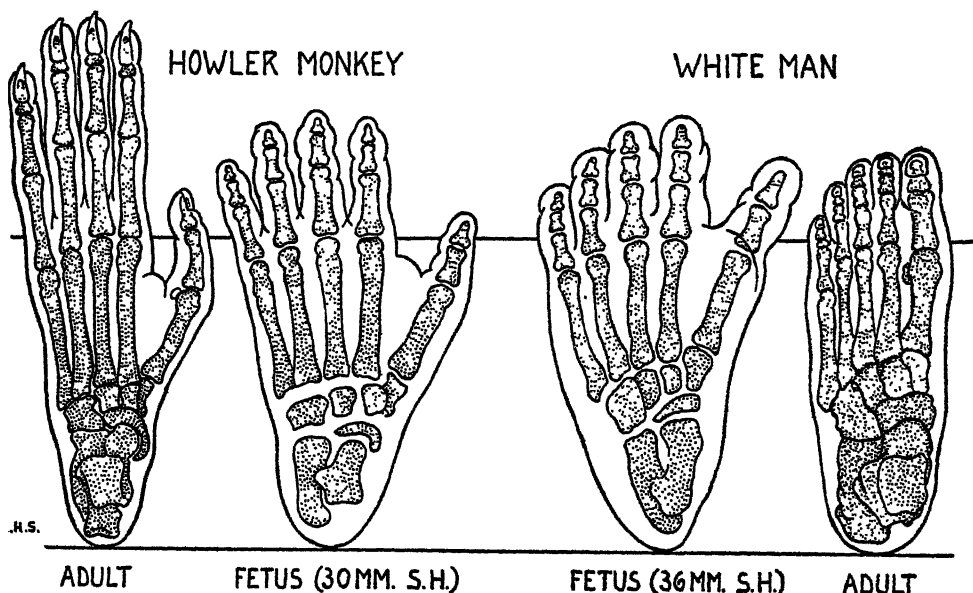


FIG. 13. DIAGRAMS OF THE GROWTH CHANGES IN THE FOOT OF MAN AND OF A MONKEY (*Alouatta seniculus maccormelli*)

The four feet are reduced to the same distance from the heel to the second metatarso-phalangeal joint.

the great toe in gorilla were chiefly obtained from measurements on plaster casts and on illustrations and are therefore only approximate: fetus (Duckworth, 1904) 82.1; older fetus (Deniker, 1885) 87.2; 3 year old female (cast of foot of "Dinah," lent by Dr. McGregor) 74.3; 3½ year old male ("John Daniel II," measured alive by the author) 83.8; 5 year old male (cast of foot of "John Daniel I," donated by Dr. McGregor) 82.2; adult female (cast of foot by Mr.

average 62.5 in 3 fetuses of an advanced state of development, 59.4 in 5 infantile (preserved) specimens, and 52.1 in 2 adults (casts).

In man this index (foot length to 3rd toe!) amounts to about 95 in fetuses of the 3rd month and in adults it varies between 98.5 and 108.5.

In all primate embryos the great toe, just after its appearance on the foot plate, is found to branch from the sole very close to the base of the second toe. In

all monkeys and apes this place of branching shifts proximally in the course of growth, toward a place nearer the ankle, just as the thumb moves ontogenetically away from the base of the index finger. However, both these rules have their exceptions. For the thumb it exists, as discussed above, in most of the platyrrhine monkeys, which retain the fetal condition to adult life, in regard to the great toe it is man, who behaves in an exceptional way, since his great toe does not shift its place of attachment but remains in its typically fetal position at all stages of growth. Among adult monkeys the great

with the intermediate medial edge of the sole form diagrammatically a U, rather than a V, as in man. The degree of opposability of the hallux is much more perfect in orang and chimpanzee than in the adult East-African gorilla and, of course, than in man. There is some embryological evidence which can be claimed as support for the assumption that the human pedigree contains forms with an at least partly opposable great toe. The relatively short length and markedly abducted position of the hallux in early human fetuses (see figs 9, 12 and 13) may be quoted here and then particu-



FIG 14 FEET OF ADULT OR NEARLY ADULT ANTHROPOID APES AND MAN (ORANG AFTER A SPECIMEN IN THE AUTHOR'S COLLECTION, CHIMPANZEE AFTER SCHLAGINHAUFEN, 1911, FIRST GORILLA AFTER HARTMANN, 1880, SECOND GORILLA AFTER AKELEY, 1923)

toe branches from the sole at a varying but always considerable distance from the base of the second toe (see e.g., Pocock, 1926). Among adult anthropoid apes this feature differs least from the human condition in the mountain gorilla, and most in orang-utan, with a greater discrepancy between the latter two than between gorilla and man (see figure 14). There can be no question that the opposability of the great toe is greatly facilitated by its branching at a place which is removed from the second toe, so that, in the act of grasping, these toes together

early the investigations of Straus (1927), who found a somewhat greater rotation in the sense of opposability in the first metatarsal of early human fetuses than in that of adult man.

Heel

To this discussion on the foot must be added a few remarks concerning the heel. In all monkeys the profile of the heel forms a practically straight line running smoothly from the calf to where it bends over to the sole. Among the anthropoid apes, especially in gorilla, one encounters

for the first time indications of a prominent heel, i.e., a heel which projects beyond the profile of the ankle region. In human races the degree of prominence of the heel is much more developed in the negro than in the white, indeed, this forms a most striking racial difference even in fetuses. Negro fetuses from the 5th or 6th month to term can, as a rule, be readily identified by their characteristic heel. By dissecting a considerable number of white and negro heels in fetuses and in adults the author found the projecting heel to be caused entirely by a thick layer of subcutaneous fat and not to be due to any greater length of the

metatarsals, has demonstrated that there exists a certain correlation between the size of corresponding parts of fore- and hind-limb in monkeys and apes, a condition which he called the homotypy of proportions. One instance suffices to illustrate this correlation. Primates with unusually long hands, such as orang-utan, also possess very long feet. P. and F. Sarasin (1892-93) had called attention to the fact that human races with a relatively long forearm have also a proportionately long leg and *vice versa*. To these zoological and anthropological results can now be added those of an embryological nature and it will be found

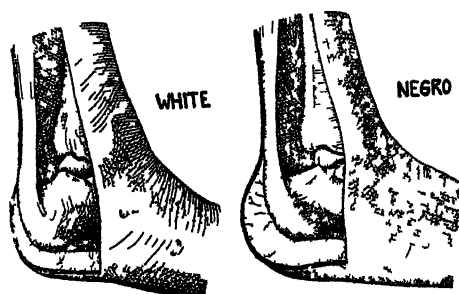


FIG. 15. PARTIAL DISSECTION OF THE HEEL IN AN ADULT WHITE AND IN AN ADULT NEGRO, SHOWING THE MUCH THICKER LAYER OF SUBCUTANEOUS TISSUE IN THE LATTER THAN IN THE FORMER.

corpus calcanei in negroes than in whites (see fig. 15). The subcutaneous tissue in the heel region of monkeys is proportionately much less developed than in white man and does not extend far up on the tuber calcanei. Why the negro heel should be padded even to some distance above the tuber calcanei is difficult to understand. Underneath the heel this subcutaneous padding serves as a sort of shock absorber in walking.

VII. ANALOGIES IN THE GROWTH OF UPPER AND LOWER LIMB

Mollison (1911), in an excellent monograph on the body proportions of pri-

TABLE 17
Growth changes in whites in the leg foot and forearm-hand proportion

	FOOT LENGTH	
Fetuses, 9th week	139.2	118.4
Fetuses, 10th week	107.0	91.0
Fetuses, 15th week	79.1	71.3
Newborns	97.5	94.8
Adult males	68.7	74.9

that they all agree in pointing to rather close analogies, or a certain parallelism, in the phylogeny as well as the ontogeny of the upper and lower extremities.

The age changes in the relative lengths of the limbs, as illustrated by the curves in figure 8, show probably clearer than anything else the close correlation between upper and lower limb during growth. From table 11 it is evident that both the upper arm-forearm proportion and that between thigh and leg is altered between fetal and adult life in a very similar way and that both these corresponding indices are always larger in

negroes than in whites. A comparison between the leg-foot proportion (given in figure 3) with the relation in length between the corresponding parts of the upper limb, the forearm and hand (contained in figure 4) reveals the fact that the very striking growth changes in these proportions agree in principle very closely, since in both indices there occurs first a marked and rapid decrease, changing after the 15th week of fetal life into an increase, and after birth changing back again to a second decrease (see table 17). Finally,

other proportion on the body. This holds true in regard to fetuses as well as in regard to adults (see table 27).

VIII. HEAD

Relative size of brain part of head

It is a general and well established rule for vertebrates that in related animals the relative brain size decreases as the body size increases. This is sometimes referred to as Haller's law. Of the many authors, who have collected data in support of

TABLE 18

Growth changes in the relative head size (average head diameter in percentage of anterior trunk height) of primates. The indices for man are approximate means, those for apes and monkeys are based upon single specimens or, where two numbers are given, they represent the range of variation of two or more specimens. The indices for the chimpanzees were obtained from data by Friedenthal (1914), except those for the nearly newborn and the infantile specimen

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th-5th	6th-8th	9th-10th	Infant	Juvenile	Adult
Man (Whites).....	85.0	78.0	69.0	59.0			31.0
Chimpanzee.....		59.8	60.4	49.5	39.0	34.6	28.5
Orang-utan.....		65.0	63.8-64.9	60.7	56.9-60.2	49.0	31.8
Gibbon.....	61.4-67.6	62.4-64.9	63.4-64.5	60.8-60.9	52.5-59.6	48.8	30.2-33.3
Baboon.....		55.0	57.5-51.3	56.3-57.0	55.7	38.3-39.8	30.6-34.5
Macaque.....		57.5	54.8-54.8	51.9	34.1-40.2	26.8-27.0	23.5-27.5
Proboscis monkey.....			48.9-50.3	44.0			18.5
Colobus monkey.....		49.7	49.6-51.4	47.3			20.1
Capuchin monkey.....		63.2	70.9		50.6	38.7-44.4	30.9
Howler monkey.....	67.7-73.3	59.6-62.6	54.6-57.5	49.1-54.3	46.2-49.0	30.2-37.7	26.6-27.1
Spider monkey.....				51.3-56.0	47.3-51.9	38.5-43.8	24.4-31.7

both the hand and the foot become relatively much narrower with advance in growth (see fig. 9) and both these parts are slightly narrower in negroes than in whites.

It is most likely directly due to this close analogy in the growth of the upper and lower limb that the proportion between these limbs (intermembral index) is very much more constant than the proportion between either of the two limb lengths and the trunk height. As a matter of fact, the intermembral index varies individually less than almost any

this rule, only a few may be mentioned here, namely Weber (1896), Dubois (1897, 1914), Brandt (1898), Hrdlička (1905, 1925 b), Lapique (1909), and Funk (1911). A clear example for illustrating this relation between relative brain size and body size is found in a comparison between house cat and lion: Of the 3,300 grams body weight in the former the brain forms 0.94 per cent, while of the 119,500 grams body weight of the latter the brain constitutes only 0.18 per cent. Among primates it is also found that by and large the smaller the species the proportion-

ately larger is the brain. The following figures (brain weight in percentage of body weight, calculated from data of Dubois, 1914) suffice to demonstrate this: orang-utan (73,500 grams) 0.54, gibbon (9,500 grams) 1.37, marmoset (335 grams) 3.82. The relative brain weight of adult man (white males 2.18) is surpassed by that of many small monkeys but is much higher than that of any of the large apes.

The influence of body size on the relative size of the brain is also noticed in

part of the head decreases in all vertebrates as the individual grows to larger size. For instance, the arithmetic mean of head length, breadth, and height (head module), expressed in percentage of the trunk height, amounts on an average to 95.5 in human fetuses of the 9th week, but in adult man this proportion has decreased to 31.1. According to table 18, other primates show very similar changes. It is interesting to note that the decrease in this index may proceed during correspond-

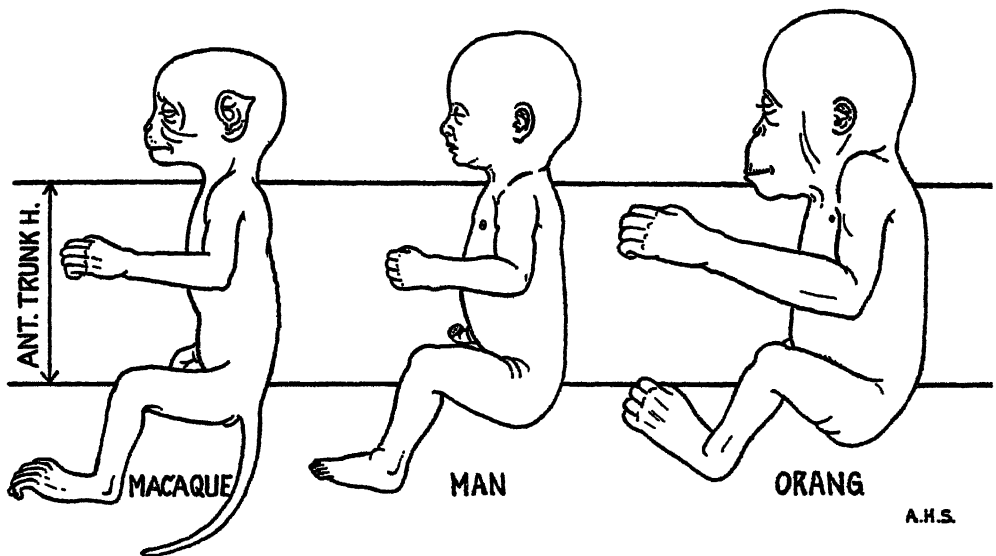


FIG. 16. BODY PROPORTIONS IN NEWBORN MACAQUE, MAN, AND ORANG-UTAN; ALL REDUCED TO THE SAME ANTERIOR TRUNK HEIGHT

Note the different sizes of the brain part of the head

the different human races, since pygmies have in general proportionately larger heads than the tall races. Indeed, it can even be demonstrated within a race, as was done for whites, e.g., by Hrdlička (1925 a) and for American Indians by the author (1926 a).

These introductory notes form a necessary background for the discussion of the growth changes in the relative head size, since it appears that the above rule may also be applied to the conditions of development. The relative size of the brain

ing periods of development with different intensity in different primates. For instance, in the orang-utan and in the gibbon the prenatal decrease is very much smaller than in man, so that at birth these apes have a proportionately larger head than newborn babies. That the latter fall well within the range of variation of the relative head size among newborn monkeys and apes is also shown by figure 16.

In conclusion it may be stated that the large proportionate size of the brain part

of the head in primate fetuses, which is directly responsible for their high forehead, is of no phylogenetic significance. In other words, it can not support theories, such as have been advanced by Kollmann (1905), Klaatsch (1923), and Hill-Tout (1921, 1924), but is due to specific conditions of growth, common to all vertebrates.

Cephalic index

The cephalic index, which expresses the proportion between the breadth and the length of the brain part of the head, undergoes a marked decrease in the course of human fetal growth (see fig. 20). In young fetuses these two head diameters may be nearly alike, i.e., the maximum value of the index is still as high as 98. According to tables 19 and 20, a dolichocephalic index, indicating a very long and narrow head shape, does not appear until the 6th fetal month, while the opposite extreme, or an ultrabrachycephalic index, is normally not found

9th fetal month, is of little significance since it was based upon observations on only 6 specimens. The older literature contains some reports which contrast

TABLE 19
Averages and ranges of variation of the cephalic index (head breadth in percentage of head length) in white fetuses and adults

	AVERAGE	MINIMUM	MAXIMUM
3rd month, 1st half..	87.4	81.6	98.0
3rd month, 2nd half.	86.6	77.8	96.9
4th month	87.6	76.5	97.2
5th month.....	84.9	76.7	93.0
6th month.....	82.2	74.6	89.1
7th month.....	81.3	71.6	92.1
8th month.....	81.3	74.0	87.2
9th month.....	81.5	73.5	85.3
10th month.....	79.3	71.2	90.3
Adults (100 ♂ and ♀)	77.5	69.7	86.9

sharply with the results discussed above. Welcker (1862), Rudinger (1877), and Schaeffer (1893 and 1896) obtained very low cephalic indices in fetuses. These authors had used only small series of specimens and had taken their measure-

TABLE 20
Distribution (in percentage frequencies) of the cephalic index of white fetuses and adults among the different classes of this index

INDEX	3RD FETAL MONTH	4TH-5TH FETAL MONTH	6TH-7TH FETAL MONTH	8TH-10TH FETAL MONTH	ADULTS
Dolichocephalic, x-75.9.....	0	0	7	17	22
Mesocephalic, 76.0-80.9.....	10	12	31	32	57
Brachycephalic, 81.0-85.9.....	35	27	41	41	20
Hyperbrachycephalic, 86.0-90.9.....	32	47	20	10	1
Ultrabrachycephalic, 91.0-x.....	23	14	1	0	0

after the 7th month of prenatal development. These results agree in principle with the findings of Retzius (1904). Mazzi (1918) found 71 per cent of 9 to 10 months old fetuses to be brachycephalic (average 84.3), a percentage which is even higher than that of the writer. Mazzi's further conclusion, that the cephalic index increases before the

measurements on the skull which is easily distorted and shrinks in drying very considerably, hardly ever retaining its normal shape.

From the figures in tables 19 and 20 can be concluded that dolichocephalic adults must, as a rule, have changed more during their ontogeny in regard to head shape than broad-headed adults.

Among the latter the cephalic index may undergo a slight secondary increase after birth (e.g., Tschepourkovsky, 1911). Pfitzner (1899) found this index to remain constant from birth to adult life. It can be stated, however, that in general the head index decreases during postnatal growth, as was demonstrated on very large material for instance by Porter (1894), Hrdlička (1900), and Röse (1905). This occurrence of age changes in the cephalic index has not always been considered in studies on the inheritance of this proportion.

The cephalic index of monkeys and apes seems to change very little in the course of

form the head can depart only after the skull has become more widely ossified.

Relative height of the face

The face part of the head grows faster than the brain part in man as well as in all the other primates (see fig. 17). This is most strikingly demonstrated by the so-called vertical cephalo-facial index or the proportion between the height of the face (to the naso-frontal suture) and the head height (from the ear opening), which is listed in tables 21 and 22. In the first half of the 3rd month the face height of human fetuses amounts to only 47 per-

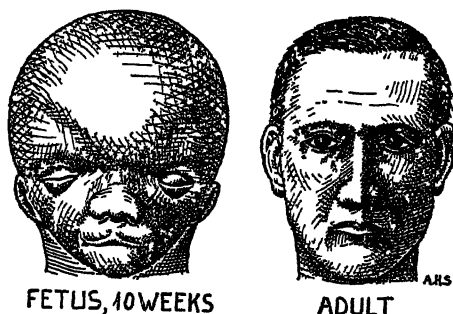


FIG. 17. FRONT VIEWS OF THE HEAD OF A HUMAN FETUS, 10 WEEKS OLD, AND OF THE HEAD OF AN ADULT MAN, BOTH REDUCED TO THE SAME TOTAL HEIGHT

growth. For instance, it ranges in gibbons between 82.5 and 90.1 in 11 fetuses, and between 84.1 and 90.8 in 7 adults. In very broad-headed monkeys the index tends even to increase with advance in age; e.g., the values for howler monkeys varied in fetuses (48 to 68 mm. sitting height) from 84.8 to 86.8 and in adults from 90.3 to 94.2.

The prenatal growth changes in the human cephalic index can not be interpreted as being of phylogenetic significance. It is much more likely that the intracranial pressure in the embryo tends to mold the soft brain part of the head into a sphere, from which approximate

TABLE 21
Averages of white and negro fetuses and adults for the proportion: Total face height in percentage of head height

3rd month, 1st half. .	47 4	
3rd month, 2nd half.	48 7	52.2
4th month.	51 2	55 2
5th month.	54 4	57.1
6th month.	55 9	57.8
7th month.	55 3	59.7
8th month.	57 0	59.2
9th month.	57 2	59.3
10th month.	58.3	60.7
Adult males.	85 4	91.7

cent of the head height, but in adult whites to 85 percent. In all adult monkeys and apes this index is very much higher than in adult man, rising with but few exceptions considerably above 100. The maximum index, of 172.6, was found in a male adult howler monkey, which surpasses the average adult white man by 87 index units. A howler monkey fetus, corresponding in development to human fetuses of the 11th week, differs from the latter by only 12 index units.

The growth changes in this proportion are much more marked after birth than during fetal life. This is chiefly due to

the comparatively late development of the masticatory apparatus, which increases the facial height tremendously during childhood.

The figures in table 21 show a marked and constant racial difference, according to which negroes have the proportionately higher face, respectively lower

The face height of the negro is also slightly greater than that of the white in its relation to the face breadth, and this, too, in fetuses as well as in adults. This height-width proportion of the face (upper face height in percentage of face breadth) remains practically unaltered during fetal growth (approximate average in whites

TABLE 22

Growth changes in the proportions: Total face height in percentage of head height. The development, but not the actual age, of the different monkey fetuses in a given perpendicular column corresponds approximately to that of human fetuses of the stated age in the particular column

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th-5th	6th-8th	9th-10th	Infant	Juvenile	Adult
Orang-utan		75 6	83 6-86 2	91 4	87 4-91 0	108 3	127 7-150 0
Gibbon	53 8-61 1	63 1-64 8	60 5-66 3	64 5-65 4	69 0-75 7	100 0-101 1	108 8-126 7
Baboon		76 2	80 2-85 3	81 0	84 7	117 5-130 6	146 1-161 8
Macaque		64 1	68 5-71 0	74 0	94 9-106 8	101 9-121 3	124 4-158 0
Capuchin monkey		71 3	68 3		77 5	83 7-92 3	95 9-109 4
Howler monkey	60 6-63 0	77 6-79 5	77 6-89 4	81 8-84 5	91 5-101 3	115 7-128 2	162 7-172 6

TABLE 23

Averages of white and negro fetuses and adults for the proportions of the nose: Relative nose height (nose height in percentage of upper face height), Relative nose breadth (nose breadth in percentage of face breadth), and Nasal index (nose breadth in percentage of nose height)

AGE	RELATIVE NOSE HEIGHT		RELATIVE NOSE BREADTH		NASAL INDEX	
	White	Negro	White	Negro	White	Negro
3rd month, 1st half	63 8		34.8		137 6	
3rd month, 2nd half	70 2	66 8	31 0	35 6	115 3	130 2
4th month	68 5	64 1	26 8	30 3	105 9	121 0
5th month	68 5	64 8	24 6	27 9	97 8	121.1
6th month	67 5	64 9	25.1	28 4	98 4	108 8
7th month	67 3	63 0	25.2	28 4	97 8	109 8
8th month	68 0	61 2	25.5	29 3	97 6	114 7
9th month	67 1	61 6	24.2	28.3	97.3	114 4
10th month	66 0	63.1	24 2	28 1	95 9	111.0
Adult males	71 3	67.0	24.6	30 5	62.1	79.6

brain part of the head, than whites. This difference is already apparent in fetuses. Since man has the lowest index of all primates and whites even lower values than negroes, it can be stated that the white race has deviated farther from the simian condition of this proportion than has the negro.

39), but changes considerably in postnatal life (average in white adults 56), when the face grows much more intensely in height than in width.

Nose

The conditions of growth of the human nose are shown in a condensed form in

table 23. In both, whites and negroes, the nose becomes in general relatively higher and narrower with advancing development, and, in consequence of this, the nasal index decreases (see also fig. 17). In the 3rd month of fetal life 98 percent of the whites are hyperchamaerrhinc, i.e., have a nasal index above 100. In the 4th

decreases during fetal growth, namely from 77 in the 3rd month to 62 at birth (Broca, 1892). The values of the latter index are much below those for the external nose on account of the difference between the nasal breadth and the width of the apertura piriformis, a difference which becomes steadily less with advanc-



FIG. 18. RACIAL DIFFERENCES BETWEEN THE HEADS OF WHITE NOS. 1 AND 3 AND NEGRO NOS. 2 AND 4 FETUSES. All four specimens about 5 months old. Note particularly the differences in the nose and in the lips.

month 84 percent of the whites still fall into this group, but in whites of the 10th month only 46 percent have retained this high index. Among adult whites there are no chamaerrhinc individuals left at all, 96 percent of the cases being leptorrhinc, i.e., having a nasal index below 70. The nasal index, formed from measurements on the bony nose, also

ing growth (Schultz, 1918 & 1920). During postnatal life the height-width proportion of the external nose continues to decrease, as has been shown by many investigators, e.g., Houzé (1888), Blind (1890), and Schwerz (1910).

In monkeys and apes the nasal index decreases with advance in growth, as in man, embryos having a proportionately

very broad nose (see e.g., figures 16 c and 22 c by Keibel, 1906). However, the decrease of the nasal index occurs in most monkeys much more rapidly than in man, so that monkey fetuses have considerably lower indices than human fetuses. In the gibbon, for instance, the nasal index amounts to 62.8 in a fetus (56 mm. sitting height) and varies between 38.7 and 42.8 in adults. The nasal index of howler monkeys was found to be 80 in a fetus (48 mm. sitting height) and anywhere from 51.9 to 58.3 in adults.

The three proportions of the nose, listed in table 23, show at all growth

The nasal index decreases ontogenetically to much lower values in whites than in negroes. The nose of the latter, therefore, is broader than that of the former not only in relation to the face breadth but also in proportion to the nose height. The nose of the adult negro has in every respect deviated less from the human fetal nose than has the adult white nose. The latter has advanced ontogenetically as well as phylogenetically to the highest development, whereas the nose in such races as the Australians and the Bushmen represents the most primitive and least specialized condition in man.

TABLE 24

Growth changes in the proportion: Interocular breadth in percentage of face breadth. The indices for man are approximate means, those for other primates are based upon single specimens or, where two numbers are given, they represent the range of variation of two or more specimens

PRIMATE	Age						
	Prenatal (month)				Postnatal		
	3rd	4th-5th	6th-8th	9th-10th	Infant	Juvenile	Adult
Man (Whites).....	44 0	32 0	27.5	25 0		24 3	23 0
Orang-utan.....		29 3	15 4-18.5	19 1	11 8-18 7	12 2-20 1	12 0
Gibbon.....	65 7-34 0	25 7-30.0	23.4-28.5	24 4-26 5	20 7-25.6	20 4-23 8	18.6-27.2
Baboon.....		26 8	19 0-20 9	18 0-18 3	15.3-15 6	12 5-15 1	17.9
Macaque...		21.3	18.0-24 1	21 5	15 9-21.5	12 3-16 7	15 1-15 6
Colobus monkey		25 2	22.3-23.6	22 5		20.2	26 6
Capuchin monkey....		24.5	24 6		19.3	17.6-19.2	15 1-17 5
Howler monkey .	30 7-34 3	28 3-29 2	26 5-26.7	25 3-26 5	21 3-23.3	20 4-22 6	19 3-21.1
Lemur.....				48 3		46 4	44.8

stages very marked racial differences. In relation to the upper face height the nose is lower in the negro than in the white. This implies directly that the upper lip, as measured from the root of the nasal septum to the middle of the mouth, is relatively higher in the former race than in the latter. The nasal breadth, in its relation to the breadth of the face, is very much larger in negroes than in whites; even in fetuses is this racial difference unusually well marked (see fig. 18, Nos. 3 and 4; other illustrations were published by the author in 1920 and 1923a).

Relative width between the eyes

That the eyes of all primates move relatively closer together with advance in growth is shown by the decrease in the relative interocular breadth, as given in table 24. In embryonic life the relative width between the inner angles of the eye-clefts is still at least as great as in adults of most other groups of mammals. The interocular width amounts to more than half the face breadth in human fetuses of the 9th week, but in adult whites to less than one fourth (see fig. 17). The final

degree in this ontogenetic approximation of the eyes reaches different extremes in different primates. The prosimiae contain forms in which the eyes are widely separated (e.g., in the genera *Daubentonia*, *Mixocebus*, *Lemur*, *Propithecus*, and *Indris*), but other forms have very narrow inter-orbital regions, particularly the genera *Tarsius* and *Loris*. Among the monkeys and apes the eyes have moved relatively closest together in some Capuchin and Guenon monkeys, in macaques and some baboons, and particularly in orang-utan. Adult man has a larger relative interocular breadth than the above named primates. In dolichocephalic whites this proportion seems to decrease ontogenetically to the smallest human values, while in Tasmanians and Hottentots it is altered least, the eyes remaining relatively farther apart than in other races of man.

There can be no doubt that in the course of evolution of the primates a migration of the eyes towards each other has taken place, very similar to that occurring in the course of growth. This particular phylogenetic process affected man somewhat less than many of the other primates (see also Schwalbe, 1899).

IX. VARIABILITY

Range of variations

In previous chapters it has been shown that human racial characters develop very early in fetal life. The question now arises, whether the individual characteristics of man also appear early in ontogeny. In other publications the author has demonstrated that such bodily features as the shape of the nose (1920), the relations between upper and lower jaw (1925b), the shape of the hand, and the relative length of the limbs (1926) vary fully as much in fetuses as in adults. That individual peculiarities do not develop during

adolescence, as is sometimes assumed, but are already clearly defined even in young fetuses, is also proved by the following examples.

Table 25 lists the relative ranges of variation in the hand index at different growth stages. The extreme individual values of this index differ from each other in fetuses for as much as 36.8 percent of the average value. Generally speaking, the shape of the hand tends to vary with

TABLE 25

Relative ranges of variation (difference between minimum and maximum in percentage of average) in the hand index (hand breadth in percentage of hand length) of white fetuses and adults

AGE	RELATIVE RANGE	AGE	RELATIVE RANGE
9 weeks	24.5	27 weeks	6.7
10 weeks	31.2	28 weeks	22.6
11 weeks	20.9	29 weeks	2.7
12 weeks	30.3	30 weeks	18.4
13 weeks	29.0	31 weeks	14.7
14 weeks	23.8	32 weeks	12.3
15 weeks	36.8	33 weeks	16.8
16 weeks	24.1	34 weeks	21.4
17 weeks	22.7	35 weeks	8.7
18 weeks	20.6	36 weeks	20.5
19 weeks	23.8	37 weeks	17.7
20 weeks	19.7	38 weeks	23.4
21 weeks	36.2	39 weeks	23.0
22 weeks	23.8	40 weeks	16.1
23 weeks	18.5	Average for fetal life....	20.9
24 weeks	24.8		
25 weeks	16.3		
26 weeks	16.8	Adults	22.3

practically the same intensity before birth as in adult life, but it has to be emphasized that the most extreme variations occur among the fetuses. This permits the conclusion that the variations in the relative hand width of adults must be primarily of a congenital and not of an acquired nature. Special functions, as, e.g., long continued manual labor, may exert an influence on this proportion, but merely by superimposing their effect on

the natural condition (see also Brezina & Lebzelter, 1924).

Figure 19 illustrates the range of variation in the proportion between the lengths of the upper and lower limbs. The arm of fetuses (14 weeks) amounts to anywhere from 106 to 125 percent of the length of the lower limb; in adults these percentages vary only between 79 and 88. This makes it seem more than likely that persons with

whether it is merely determined by isolated extremes, if not pathological cases. Figure 20 demonstrates on the example of the cephalic index that the extreme variations are linked by an uninterrupted series of intermediate stages, which are the more numerous the closer they approach the average. The distribution and frequency of the variations in fetuses is as normal as in adults and

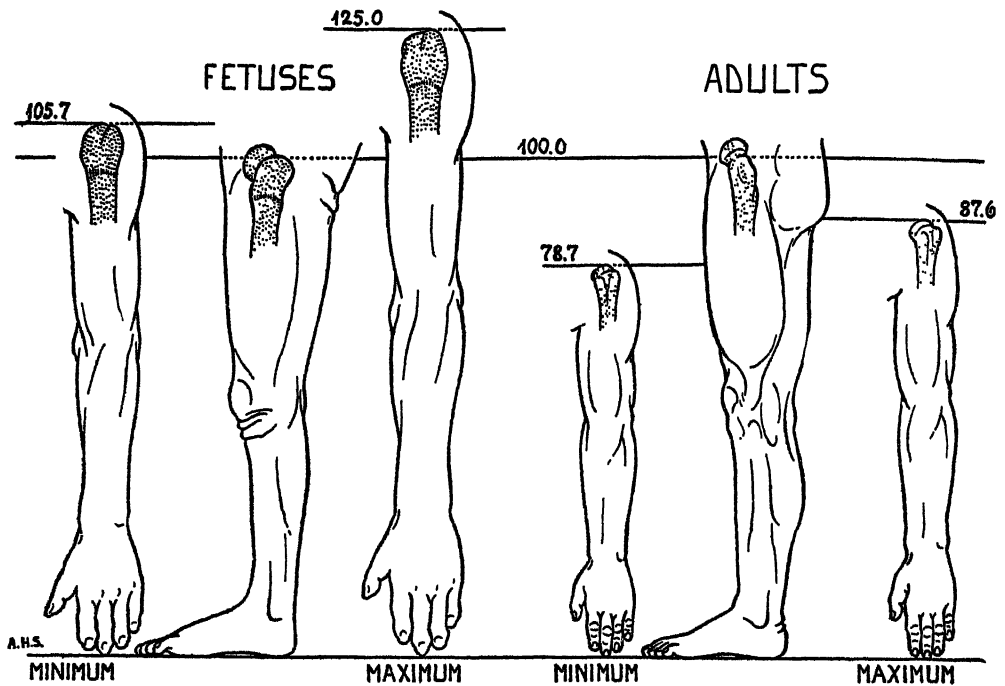


FIG. 19. DIAGRAMMATIC REPRESENTATION OF THE RANGES OF VARIATION IN THE PROPORTION BETWEEN THE TOTAL LIMB LENGTHS OF WHITE FETUSES (14TH WEEK) AND OF WHITE ADULT MEN

Total lower limb length = 100

relatively short arms, as well as those with relatively long ones, must have possessed these distinctions long before they were born and did not develop them gradually in later life.

Distribution of variations

It must be considered whether the range of variations in fetuses is really characteristic for their normal variability, or

the extremes, undoubtedly, represent the typical limits of all observed normal variations.

Variability at different ages

Fischel (1896), Mehnert (1896), and others have found a tremendous variability in early embryonic development, indeed, one which is never equalled in later growth stages. According to Minot

(1891), the variability of male guinea-pigs is more than twice as great at the beginning as at the end of postnatal growth. Pearson (1900) showed that man has a much greater variability at birth than in adult life. Woodbury (1921) found a marked decrease in human

tional exceptions have been published in more recent years (e.g. Boas & Wissler, 1905).

Variability and growth rate

Considerable evidence has been collected for an apparent correlation between

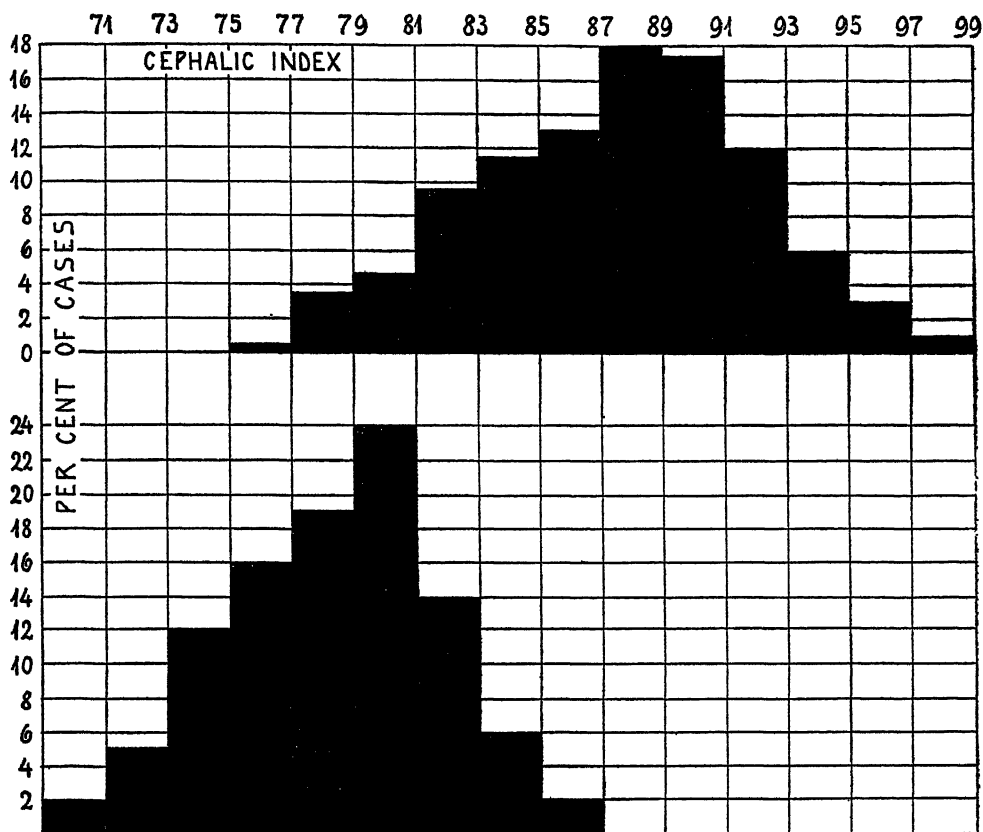


FIG. 20. FREQUENCY POLYGONS FOR THE VARIATIONS IN THE CEPHALIC INDEX (LENGTH : BREADTH PROPORTION OF THE HEAD) OF 200 WHITE FETUSES OF THE THIRD AND FOURTH MONTH (UPPER FIGURE) AND OF 100 WHITE ADULTS (LOWER FIGURE)

Both series from the population of the eastern United States (mostly from Baltimore)

variability during the first six years of postnatal life. Based upon some of the above quoted data Vernon (1903) had proposed the following law: "The variability of a developing organism diminishes regularly with its growth." Vernon himself called attention to certain exceptions to his "law," and many addi-

variability and rate of growth (Boas, 1896-07; King, 1923; and others), which would imply that the former fluctuates at different ages in accordance with the changes in intensity of the latter. This claim is largely supported by data in regard to postnatal growth. It would seem but consistent to conclude that the

high variability of the embryonic and fetal body is directly due to the rapidity of prenatal growth and that because of this it would be expected that different measurements of the body show little correlation with one another. However, the author's results do not agree with these theories, or, at least, show many exceptions to them. The rate of growth, as was discussed in a previous chapter, diminishes very rapidly with advance in fetal growth, but the variability, accord-

growth rates are 13 to 15 times smaller at the former than at the latter age. The third and last example in table 26 reveals the surprising fact that in certain cases the correlation between two dimensions of the fetal body may even be much closer during periods of rapid growth than when growth has slowed down considerably. As a matter of fact, the highest and lowest correlation coefficients for the sitting height and trunk height happen to fall exactly into the months with the largest

TABLE 26

Rate of growth (relative increment per week) and variability and rate of growth and correlation in various measurements and proportions of white fetuses and adults. The increments and coefficients have been calculated for each week of fetal life. For a clear survey of these figures only the monthly averages are listed in this table

INCREMENT OR COEFFICIENT	MEASUREMENT OR PROPORTION	FETAL MONTHS								ADULT
		3rd	4th	5th	6th	7th	8th	9th	10th	
Average weekly increment....	Trunk height	29.2	18.0	9.5	8.2	5.7	5.0	1.6	5.4	0
	Shoulder breadth	24.3	19.3	11.1	6.2	4.8	3.5	2.4	6.2	0
Average weekly variation coefficient.....	$\frac{\text{Shoulder breadth}}{\text{Trunk height}} \times 100$	6.5	8.0	9.6	8.7	7.3	3.3	4.3	5.9	8.1
Average weekly increment....	Upper limb length	39.3	23.3	11.1	5.8	4.5	2.5	3.1	4.4	0
	Lower limb length	45.5	24.2	12.3	6.9	4.1	2.9	3.1	4.0	0
Average weekly variation coefficient.....	$\frac{\text{Upper limb length}}{\text{Lower limb length}} \times 100$	3.9	3.2	3.2	3.0	2.7	1.9	3.6	3.0	2.8
Average weekly increment....	Sitting height	26.7	17.6	9.7	6.4	4.9	3.1	3.0	3.8	0
	Trunk height	29.2	18.0	9.5	8.2	5.7	5.0	1.6	5.3	0
Average weekly correlation coefficient.....	Sitting height and trunk height	+	+	+	+	+	+	-	+	+
		0.83	0.71	0.42	0.28	0.24	0.18	0.33	0.08	0.73

ing to table 26, does not change in a similar manner. For instance, the largest variation coefficients of the relative shoulder breadth occur in the 5th month, while the measurements, from which this proportion is formed, grow fastest in the 3rd month. The variability in the intermembral index decreases from the 3rd to the 8th months in close connection with the growth rate, but in the 9th month the variability is again nearly as high as in the 3rd month, though the

and smallest relative increments in these measurements.

Variability in different parts of the body

How widely the various body parts and proportions may differ in regard to their variability is demonstrated by the figures in table 27. While a few proportions are more variable in adults than in fetuses, the majority of the proportions show a greater variability before birth than at the completion of growth. However, these

age changes generally do not alter the relative degree of variability in a given proportion. Thus it is found, e.g., that the relation between the upper and the lower limb length has the smallest variation coefficients in both columns of table 27, and that the relative position of the umbilicus is the most variable feature of both fetuses and adults. On account of all these and certain other findings the author tends to agree with Peter (1920), who reached the conclusion that there exists a typical variability for each species,

Compensating variations

Of particular interest in this connection is the fact that the total lengths of the extremities are more constant than their component parts. For instance, the relative range of variation of the total upper limb length (got by adding the lengths of upper arm, forearm, and hand) averages in fetuses of corresponding sitting height 8.5, but the relative range of the upper arm length amounts to 9.9, that of the forearm length to 9.2, and that of the hand

TABLE 27

Variation coefficients and their probable errors for various body proportions of white fetuses and adults. The figures for fetuses represent the averages of 32 weekly coefficients

PROPORTION	FETUSES	ADULTS
Shoulder breadth : anterior trunk height.....	6.69 \pm 0.96	8.06 \pm 0.78
Hip breadth : anterior trunk height.....	7.29 \pm 1.09	6.18 \pm 0.60
Relative position of umbilicus	13.34 \pm 2.07	9.40 \pm 0.91
Total upper limb length : anterior trunk height.....	7.04 \pm 1.06	5.82 \pm 0.57
Total lower limb length : anterior trunk height.....	7.18 \pm 1.09	5.57 \pm 0.54
Total upper limb length : total lower limb length.....	3.05 \pm 0.48	2.75 \pm 0.27
Forearm length : upper arm length.....	4.24 \pm 0.64	6.14 \pm 0.60
Leg length : thigh length.....	4.24 \pm 0.63	4.60 \pm 0.45
Average head diameter : anterior trunk height.....	6.59 \pm 0.99	4.86 \pm 0.47
Head breadth : head length.....	4.45 \pm 0.66	4.31 \pm 0.42
Total face height : anterior trunk height.....	7.29 \pm 1.10	6.77 \pm 0.66
Upper face height : average head circumference.....	5.74 \pm 0.86	6.87 \pm 0.62
Upper face height : face breadth.....	6.70 \pm 1.03	7.72 \pm 0.75
Nose breadth : nose height.....	7.77 \pm 1.20	7.76 \pm 0.75
Average of all (14) proportions.....	6.54	6.20

each bodily character, and each stage of development. Markedly different variabilities in different species of primates have been described by the author in another paper (1926).

The variability of absolute dimensions on the fetal body can be determined only on specimens of exactly the same age, i.e., size, in order to exclude individual differences due to growth. It suffices to state, that the absolute measurements of fetuses with the same sitting height were found to vary with different intensity in different parts of the body, just as various proportions have different variabilities.

length to 11.2. This must be interpreted as indicating that an individual lengthening of one part of an extremity tends to be compensated for by a relative shortening in another part of the same extremity and *vice versa*. In other words, an acceleration of growth in one segment of a limb must generally be accompanied by retarded growth in another segment. This may be termed "the rule of compensating variations." That this rule is applicable also in regard to adults is apparent from figures, recently published by Todd (1925). This author obtained the following variation coefficients: Total upper limb length

than in adult life. In ear size there exists no preference, as in the first two measurements, of one side over the other, at least according to the author's findings. In adults Worobjew (1901) found the right ear to be more frequently the larger of the two, but Godin (1910) obtained just the opposite result.

Many more asymmetries exist in other parts of the fetal body, e.g., in the length of the clavicles and in the exact position of the nipples. All these asymmetries are manifestations of a certain independence in the growth of the two halves of one and the same body.

ations are present long before environment could possibly play an important rôle.

A comparison between the variabilities existing in different age groups has one uncertain factor with which to reckon and that is mortality. It is not unthinkable that extreme variations are more likely to die at an early age than variations close to the average. This would tend to reduce the relative range of congenital variations with advance in age. It might be argued, therefore, that the wide range in the variations of some bodily characters of fetuses is subsequently diminished exclusively on account of selective mor-

TABLE 29

Percentage frequencies of symmetry and asymmetries and average differences (including cases of symmetry) between measurements on the two sides (expressed in percentage of smaller measurement) in fetuses and adults

MEASUREMENT	AGE	CASES	Right > left	Right = left	Right < left	AVERAGE PER CENT DIFFERENCE
Humerus length.....	Fetal	100	52	27	21	1.3
	Adult	105	54	24	22	1.5
Foot length.....	Fetal	100	33	20	47	1.4
	Adult	500	31	16	53	1.1
Ear height.....	Fetal	100	39	25	36	2.9
	Adult	100	33	37	30	1.9

Conclusions in regard to variability

It has been shown that not only individuals but even the right and left halves of one body vary no less—indeed, in some cases more—before birth than in adult life. It was demonstrated, furthermore, that at any stage of growth different bodily characteristics have different degrees of variability and that, generally speaking, these typical degrees seem to maintain their relation to each other throughout development. An analysis of these findings leads inevitably to the conclusion that the influence of environmental factors can not be very large and, hence, has often been much overestimated. Vari-

ality. Certainly the prenatal death rate eliminates a very large percentage of all variations. From a survey of the literature on this question the author (1921) has reached the conservative conclusion that at most 78 out of every 100 conceptions develop to term. It has to be emphasized that, whereas this explanation is not impossible, it is one which at present can be neither effectively supported nor entirely disproved.

X. SUMMARY

Much could be added to this review of fetal growth, which is far from complete. The data presented were selected particularly from the point of view of the phys-

MEASUREMENT	GENERAL TREND OF RELATIVE CHANGE WITH ADVANCING AGE IN MAN	AVERAGES OF PROPORTION IN WHITES			GENERAL TREND OF RELATIVE CHANGE WITH ADVANCING AGE IN APES AND MONKEYS
		Fetus, 9th week	New- born	Adult	
Chest circumference.....	Decreases in relation to trunk height	238	179	170	In principle the same as in man
Hip breadth.....	Increases in relation to trunk height	42	54	62	In principle the same as in man
Hip breadth.....	Increases in relation to shoulder breadth	58	84	91	In principle the same as in man
Transverse chest diameter.....	Increases in relation to sagittal chest diameter	105	119	130	The same as in man, in apes, but opposite in monkeys
Position of umbilicus.....	Shifts to a relatively higher place on the trunk	16	24	30	The same as in man
Position of nipples.....	Shifts to a relatively lower place on the trunk except during 6th-10th month of fetal life	80	81	73	Shifts to a relatively higher place on the trunk, i.e., in the opposite direction as in man
Total length of upper limb.....	Increases in relation to trunk height, except during 6th-10th month of fetal life (decrease)	96	122	145	Principally similar increase and decrease as in man
Total length of upper limb.....	Decrease in relation to total length of lower limb	133	105	83	The same as in man, though not as pronounced
Total length of lower limb.....	Increases in relation to trunk height, except during 6th-10th month of fetal life (decrease)	72	116	175	Principally similar increase and decrease as in man, though changes not as pronounced
Forearm length.....	Increases in relation to upper arm length	72	79	84	The same as in man, though mostly more pronounced
Leg length.....	Increases in relation to thigh length	65	79	84	The same as in man or no change
Hand breadth.....	Decreases in relation to hand length	60	53	45	The same as in man
Foot breadth.....	Decreases in relation to foot length	52	41	37	The same as in man
Thumb length.....	Decreases in relation to hand length, except during postnatal life	74	68	69	The same as in man
Average head diameter.....	Decreases in relation to trunk height	95	59	31	The same as in man
Head breadth.....	Decreases in relation to head length	87	79	77	Mostly no change or sometimes slight change in opposite direction
Total face height.....	Increases in relation to head height	47	58	85	The same as in man but mostly more marked
Upper face height.....	Increases in relation to face breadth (decreases slightly before birth)	40	38	56	Generally increases as in postnatal life of man
Nose breadth.....	Decreases in relation to face breadth	36	24	25	In principle the same as in man
Nose breadth.....	Decreases in relation to nose height	145	96	62	In principle the same as in man but proceeding more rapidly in most cases
Interocular breadth.....	Decreases in relation to face breadth	52	25	23	In principle the same as in man

ical anthropologist and in the hope that they may be found useful primarily in the search for the laws governing individual growth and, indirectly, also in connection with the study of the evolutionary specializations in races and species. In spite of the fact that the scope of this paper has been limited, it has been possible to sketch merely the outlines of the many different and often very complicated conditions of fetal growth. To summarize fully this review, which already has had

these changes differ frequently in the various species. The different proportions become altered in the course of growth with widely differing intensity. For instance, in man, according to the averages in table 30, the relative head size changes most (from 95 to 31), the relative length of the lower limb (72 to 175) and the nasal index (145 to 62) change almost as much; however, some other proportions, such as the relative thumb length (74 to 69), are but little different in early and late

TABLE 31

Racial differences between whites and negroes, existing in fetal as well as in adult life. A racial condition marked with is somewhat more "simian" and less "human" than in the other race*

BODILY CHARACTER	IN WHITES (AS COMPARED WITH NEGROES)	IN NEGROES (AS COMPARED WITH WHITES)
Hip breadth in relation to shoulder breadth.....	Broader	Narrower
Total length of upper limb in relation to trunk height.	Slightly shorter	Slightly longer
Total length of upper limb in relation to total length of lower limb.....	Slightly shorter	Slightly longer*
Forearm length in relation to upper arm length.....	Shorter	Longer*
Hand breadth in relation to hand length.....	Broader	Narrower*
Thumb length in relation to hand length.....	Longer	Shorter*
Finger II longer than finger IV.....	Not rare	Very rare*
Total length of lower limb in relation to trunk height.	Slightly shorter*	Slightly longer
Leg length in relation to thigh length.....	Shorter	Longer*
Foot breadth in relation to foot length.....	Slightly broader	Slightly narrower*
Great toe longer than second toe.....	Frequent	Rare*
Heel prominent.....	Rare*	Very frequent
Total face height in relation to head height.....	Lower	Higher*
Nose breadth in relation to face breadth.....	Much narrower*	Much broader
Nose breadth in relation to nose height.....	Very much narrower*	Very much broader
Upper lip in relation to upper face height.....	Lower	Higher
Lips very thick.....	Never*	Practically always

to be condensed to the point of dryness, would entail an undue amount of repetition. This chapter, therefore, is restricted chiefly to the tabulation of the general trend of the growth changes in the most important body proportions (table 30) and to the list of racial differences existing before birth (table 31). These tables illustrate a few generalizations which have not been mentioned above: The majority of the proportions change ontogenetically in a very similar manner in all primates, but the rapidity and the final degree of

stages of development. How much the degree of ontogenetic change differs in the various body parts, is also clearly shown by the series of diagrammatic illustrations of the exact body proportions in human fetuses and in an adult (drawn under the author's direction), which have been published in Gray's textbook of human anatomy (21st edition, 1924, fig. 57). All these conditions can be traced to the fact that the rate of growth changes with age and differs in the various parts of the body. This, of course, is not an explana-

tion but merely points in the direction in which the ultimate causes are to be sought.

In nine of the bodily characters which show racial differences in fetuses, the whites are more peculiarly human than the negroes; in five other characters, however, this relation is reversed and the negroes are farther removed than the whites from the typically simian conditions (table 31). Incidentally, it should be kept in mind that the term "simian" is not synonymous with "primitive." For instance, the thumb in many respects is more simian in the negro but more primitive or original in the white.

Finally, it has to be mentioned that no racial differences exist in fetuses which are not also present in adults.

XI. GENERAL CONCLUSIONS

In the individual development of different human races or of different primate species, as well as in their evolution, there are theoretically only three kinds of changes possible: The changes may proceed in opposite directions, i.e., their courses may be divergent, or they may occur strictly parallel to each other, or finally, they may converge, thereby reducing the racial or species difference with advance in growth or in evolution. The studies discussed in this paper have not produced a single instance in which the ontogenetic

changes converged, either in different human races or in different primates. All human racial differences and all differences between man and apes or monkeys increase during some periods of growth and remain the same during other periods, but they never become less with advancing development. This, undoubtedly, constitutes a strong support for the assumption of a monophyletic origin of the human races and of one common ancestry for all the primates. The much closer resemblance between man, ape, and monkey in early developmental stages than in adult life, can actually not be understood in any other way than by assuming one origin for all from which they inherited the tendency for the same ontogenetic processes, which, in turn, could only have become modified through later specializations. There exists ample evidence for the conclusion that many parts of the human body are less specialized than the corresponding parts of some other primates and hence have remained phylogenetically, as well as ontogenetically, more original and primitive. In a very similar way, it can be stated that the various races of man have become specialized in the different parts of their bodies in widely differing degrees. These relative degrees of evolutionary modification correspond in many instances to the relative extent of the ontogenetic change in the particular structure.

LIST OF LITERATURE

- AHLFELD, F. 1871. Bestimmungen der Grösse und des Alters der Frucht vor der Geburt. *Arch. f. Gynäkol.*, ii, 353-372.
- AKELBY, C. E. 1923. Gorillas—real and mythical. *Natural History*, xxiii, 428-447.
- AKIBA, T. 1924. Ueber die Körperproportionen der japanischen Feten. *Folia Anatom. Japonica*, ii, 189-219.
- AREY, L. B. 1925. Simple formulae for estimating the age and size of human embryos. *Anatom. Rec.*, xxx, 289-296.
- BALDWIN, B. T. 1921. The physical growth of children from birth to maturity. *Univ. of Iowa Studies in Child Welfare*, i, No. 1.
- BARTELMER, G. W., and H. M. EVANS. 1926. Development of the human embryo during the period of somite formation, including embryos with 2 to 16 pairs of somites. *Contribut. to Embryol.*, xvii, 1-67. *Carnegie Instit.*, Washington, Publ. No. 362.
- BEAN, R. B. 1922. The sitting height. *Amer. J. of Phys. Anthropol.*, v, 349-390.

- BEAN, R. B. 1923. Alternation in growth. *Anatom. Rec.*, xxv, 119.
- . 1924. The pulse of growth in man. *Anatom. Rec.*, xxviii, 45–61.
- BEDDARD, F. E. 1893. Contributions to the anatomy of the anthropoid apes. *Transact. Zoolog. Soc.*, London, xiii, 177–218.
- BLIND, H. 1890. Ueber Nasenbildungen bei Neugeborenen. *Inaug.-Diss.*, München.
- BLUNTSCHLI, H. 1913. Demonstration zur Entwicklungsgeschichte platyrrhiner Affen, . . . *Anatom. Anz.*, xlv, Ergzh., 196.
- BOAS, F. 1896–97. The growth of Toronto school children. Report, U. S. Commissioner of Education, Washington.
- BOAS, F., and C. WISSLER. 1905. Statistics of growth. Report, U. S. Commissioner of Education, Washington. Chapter II.
- BOULE, M. 1911–13. L'homme fossile de la Chapelle-aux-Saints. *Annales de Paléontol.*, vi, 109; vii, 21, 101; viii, 209.
- BRANDT, A. 1898. Das Hirngewicht und die Zahl der peripherischen Nervenfasern in ihrer Beziehung zur Körpergrösse. *Biolog. Zentralbl.*, xviii.
- BREZINA, E., and V. LEBZELTER. 1924. Der Einfluss des Wachstums und des Berufes auf die Dimensionen der Hand. *Zeitschr. f. Konstitutionslehre*, x, 381–389.
- BROCA, P. 1872. Recherches sur l'indice nasal. *Revue d'Anthrop.*, i, 1.
- BURTSCHER, H. 1877. Das Wachstum der Extremitäten beim Menschen und bei Säugetieren vor der Geburt. *Zeitschr. f. Anat. u. Entwicklungsgesch.*, ii, 357–374.
- CALDERINI, G. 1875. Le dimensioni del feto negli ultimi tre mesi della gravidanza. Torino.
- CALKINS, L. A. 1922. Morphometry of the human fetus with special reference to the obstetric measurements of the head. *Amer. J. of Obstet. and Gynecol.*, iv.
- CHILD, C. M. 1915. Senescence and Rejuvenescence. Univ. of Chicago Press.
- DAFFNER, F. 1902. Das Wachstum des Menschen. *Anthropologische Studie*. Leipzig.
- DENIKER, J. 1884. Sur un foetus de Gorille. *Compt. Rend. Acad. Paris*, 753–756.
- . 1885. Recherches anatomiques et embryologiques sur les singes anthropoïdes. Foetus de Gorille et de Gibbon comparés aux foetus humains et aux anthropoïdes jeunes et adultes. *Arch. de Zoologie experim. et gén.*, 2^e sér., iii, Suppl., 3^e mém. 1–265.
- DUBOIS, E. 1897. Abhängigkeit des Hirngewichtes von der Körpergrösse bei den Säugetieren. *Arch. f. Anthrop.*, xxv, 1–28.
- . 1914. Die gesetzmässige Beziehung von Gehirnmasse zu Körpergrösse bei den Wirbeltieren. *Zeitschr. f. Morphol. u. Anthrop.*, xviii, 323–350.
- DUCKWORTH, W. L. H. 1904. Description of a foetus of *Gorilla savages*. *Studies from the Anthropol. Lab.*, Anatom. School, Cambridge, 11–18.
- ECKER, A. 1875. Einige Bemerkungen über einen schwankenden Charakter in der Hand des Menschen. *Arch. f. Anthrop.*, viii, 67–74.
- ELLIOT, D. G. 1913. A Review of the Primates. Monograph I, Amer. Mus. of Nat. Hist., New York.
- FAUCON, A. 1897. Pesées et mensurations fœtales à différents âges de la grossesse. Thèse, Paris.
- FÉRÉ, C. 1900. Notes sur les mains et les empreintes digitales de quelques singes. *Journ. de l'Anat. et de la Physiol.*, xxxvi, 255–267.
- FESSER, V. 1873. Die Gewichts- und Längenverhältnisse der menschlichen Früchte in verschiedenen Schwangerschaftsmonaten. *Diss.*, Breslau.
- FISCHER, A. 1896. Ueber Variabilität und Wachstum des embryonalen Körpers. *Morph. Jahrb.*, xxiv, 369–404.
- FRÉDÉRIC, J. 1903. Untersuchungen über die Sinushaare der Affen. . . . *Zeitschr. f. Morphol. u. Anthrop.*, viii, 239–275.
- FRIEDENTHAL, H. 1911. Daten und Tabellen betreffend die Gewichtszunahme des Menschen und anderer Tierarten. Arbeiten aus dem Gebiet d. experim. Physiol., Jena.
- . 1913. Papuafötus. *Zeitschr. f. Ethnol.*, xlv, 613.
- . 1914. Allgemeine und spezielle Physiologie des Menschenwachstums. Berlin.
- FUNK, K. 1911. Ueber das absolute und relative Hirngewicht bei Tieren. *Diss.*, Würzburg.
- GARTNER, R. 1922. Ueber das Wachstum der Tiere. Eine biologische Studie, unter besonderer Berücksichtigung der Haustiere. *Landwirtsch. Jahrb.*, lvii, 707–763.
- GAUFF, E. 1909. Die normalen Asymmetrien des menschlichen Körpers. *Samml. Anatom. und Physiol. Vorträge*, H. 4. Jena.
- GODIN, P. 1903. Recherches anthropométriques sur la croissance des diverses parties du corps. Paris.
- . 1910 (a). Les proportions du corps pendant la croissance. *Bull. et Mém. de la Soc. d'Anthrop. de Paris*, 6^e sér., i, 268–297.

- CODIN, P. 1910 (b). A propos d'asymétrie auriculaire. Bull. et Mém. de la Soc. d'Anthrop. de Paris. 6^e sér., i, 254-256.
- GRAY, H. 1924. Anatomy of the Human Body. 21st edit. revised by W. H. Lewis. Philadelphia.
- GRÜNING, J. 1885. Ueber die Länge der Finger und Zehen bei einigen Völkerstämmen. Arch. f. Anthrop., xvi, 511-518.
- HAMY, E. T. 1872. Recherches sur les proportions du bras et de l'avant-bras aux différents âges de la vie. Bull. de la Soc. d'Anthrop. de Paris, 2^e sér., vii, 495-513.
- . 1880. Taille du fœtus pendant la vie intra-utérine. Progrès médical, viii, No. 9. Paris.
- Croissance intra-utérine du fœtus de race blanche et de race noire. Comp. rend. des Séances et Mém. de la Soc. Biol., 7^e sér., ii, 92-93.
- HARRISON, J. P. 1884. On the relative length of the first three toes of the human foot. J. Anthrop. Instit., London, xiii, 258-269.
- HARTMANN, R. 1880. Der Gorilla. Zoologisch-zoomorphische Untersuchungen. Leipzig.
- HAWKES, O. A. M. 1914. On the relative lengths of the first and second toes of the human foot, from the point of view of occurrence, anatomy and heredity. Journ. of Genetics, iii, 249-274.
- HECKER, C. 1866. Ueber das Gewicht des Fœtus und seiner Anhänge in den verschiedenen Monaten der Schwangerschaft. Monatsschr. f. Geburtsk., xxvii, 286-299.
- HENNING. 1879. Die Wachstumsverhältnisse der Frucht und ihrer wichtigsten Organe in den verschiedenen Monaten der Tragzeit. Arch. f. Gynäkol., xiv, 314-318.
- HILL-TOOT, C. 1921. The phylogeny of man from a new angle. Transact. Roy. Soc., Canada, xv, Sec. 2., 47-82.
- . 1924. New trends in anthropology. J. Sci. Transact., B. A. A. S., Toronto, 65-66.
- HOUZÉ, E. 1888. Recherches sur l'indice nasal. Bull. Soc. Anthropol., Bruxelles, vii, 177.
- HRDLÍČKA, A. 1900. Anthropological investigations on one thousand white and colored children of both sexes. Anthropol. Rep. N. Y. Juv. Asylum.
- . 1905. Brain weights in vertebrates. Smithsonian Misc. Coll., xlviii, 89-112.
- . 1925 (a). The Old Americans. Baltimore.
- . 1925 (b). Weight of the brain and of the internal organs in American monkeys. Amer. J. Phys. Anthropol., viii, 201-211.
- JACKSON, C. M. 1907. Is gravity the factor determining the thoracic index? Zeitschr. f. Morphol. u. Anthropol., x, 240-249.
- . 1909. On the prenatal growth of the human body and the relative growth of the various organs and parts. Amer. J. of Anatomy, ix, 119-166.
- . 1914. Morris's Human Anatomy. Philadelphia.
- JOHNSTON, H. 1904. The Uganda Protectorate. New York.
- KEIBEL, F. 1906. Die äussere Körperform und der Entwicklungsgrad der Organe bei Affenembryonen. Studien über Entwickl. u. Schädelbau; Menschenaffen. 9. Liefer., Wiesbaden.
- . 1911. Modelle eines Menschenfetus und zweier Affenfeten. Anatom. Anz., xxxviii, 15.
- KRETH, A. 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J. of Anat. & Physiol., xxxvii, 18-40.
- KING, H. D. 1923. The growth and variability in the body weight of the Norway rat. Anatom. Rec., xxv, 79-94.
- KINGSBURY, B. F. 1924. The significance of the so-called law of cephalocaudal differential growth. Anatom. Rec., xxvii, 305-321.
- . 1926. On the so-called law of antero-posterior development. Anatom. Rec., xxxiii, 73-87.
- KLAATSCH, H. 1923. The Evolution and Progress of Mankind. (Engl. Transl.) New York.
- KOLLMANN, J. 1892 (a). Beiträge zur Embryologie der Affen. Arch. f. Anatomie u. Physiol., Anatom. Abt., 137.
- KOLLMANN, J. 1892 (b). Affenembryonen aus Sumatra und Ceylon. Anatom. Anz., vii, 335.
- . 1905. Neue Gedanken über das alte Problem von der Abstammung des Menschen. Corr. Bl. Gesell. f. Anthropol., Ethnol. u. Urgesch., xxxvi, 9-20.
- KUDŌ, T. 1923. Ueber den Unterschied im Eingeweidesystem europäischer und japanischer Feten. (Kann eine Rasenembryologie bestehen?). Mitt. d. xxxi. Kongr. d. japan. anatom. Gesell., Tokyo.
- LAPICQUE, L. 1909. Le poids de l'encéphale dans les différents groupes d'oiseaux. Bull. Mus. d'Hist. Nat., Paris, No. 7, 408-412.
- LEGOU, E. 1903. Quelques considerations sur le développement du fœtus. Thèse, Paris.
- LÉON, N. 1912. Cefalometria fetal. Notas de antropometria obstétrica. Mexico.
- LEVADOUX, M. J. 1907. Variétés de l'ombilic et des ses annexes. Fac. de Méd. et de Pharm. de Toulouse, No. 711.

- LEVI, G. 1925. Wachstum und Körpergrösse. Die strukturelle Grundlage der Körpergrösse bei vollausgebildeten und im Wachstum begriffenen Tieren. *Ergebn. d. Anat. u. Entwicklungsgesch.*, xxvi, 87-342.
- LOISEL, G. 1903. Croissance comparée en poids et en longueur des foetus male et femelle dans l'espèce humaine. *C. R. Soc. de Biol., Paris*, 1235.
- LÖNNBERG, E. 1917. Mammals collected in Central Africa by Captain E. Arrhenius. *Kungl. Svenska Vetenskapsakadem. Handl.*, lviii, No. 2.
- MALL, F. P. 1910. Determination of the age of human embryos and fetuses. *Manual of Human Embryol.* (Keibel and Mall), i, 180-201.
- . 1918. On the age of human embryos. *Amer. J. of Anatomy*, xxiii, 397-422.
- MANTEGAZZA, P. 1877. Della lunghezza relativa dell' indice. *Arch. per l'Antropol.* 22.
- MARTIN, R. 1905. Die Inlandstämme der Malayischen Halbinsel. Jena.
- . 1914. *Lehrbuch der Anthropologie in systematischer Darstellung*. Jena.
- MATTEGKA, H. 1893. Ueber Asymmetrie der Extremitäten, am osteologischen Material geprüft. *Prager med. Wochenschr.*, No. 47, 567-569.
- MAUREL, E. 1888. Etude sur la longueur des deux premiers orteils dans les races mongoles. *Bull. Soc. Anthropol., Paris*, 3^e sér., xi, 437.
- MAZZI, V. 1918. Il cranio fetale ed il cranio adulto. *Arch. per l'Antropol. e la Etnol.*, xlviii, 56-123.
- MEHNERT, E. 1896. Die individuelle Variation des Wirbelthierembryo. Eine Zusammenstellung. *Morphol. Arbeiten*, v, 386-444.
- MENDES CORRÊA, A. A. 1919. Sur les proportions des membres chez le foetus. *Revue anthropol.*, xxix, 219-224.
- MEYER, A. W. 1914. Curves of prenatal growth and autocatalysis. *Arch. f. Entwicklungsmechanik d. Organismen*, xl, 497-525.
- . 1915. Fields, graphs, and other data on fetal growth. *Contribut. to Embryol.*, ii, 55-68. *Carnegie Instit., Washington, Publ. No.* 222.
- MICHAELIS, P. 1906. Altersbestimmung menschlicher Embryonen und Foeten auf Grund von Messungen. *Arch. f. Gynäkol.*, lxxviii, 267.
- MINOT, C. S. 1891. Senescence and rejuvenation. *Journ. of Physiol.*, xii, 97-153.
- MOLLISON, T. 1911. Die Körperproportionen der Primaten. *Morphol. Jahrb.*, xlii, 79-304.
- MÜLLER, C. 1906. Zur Entwicklung des menschlichen Brustkorbes. *Morphol. Jahrb.*, xxxv, 591-696.
- NABF, A. 1917. Die individuelle Entwicklung organischer Formen als Urkunde ihrer Stammesgeschichte (Kritische Betrachtungen über das sogenannte "biogenetische Grundgesetz"). Jena.
- NISHIZUKA, T. 1925. Beiträge zur Osteologie der Föten, Neugeborenen und Kinder nebst Erwachsenen (Japaner). Knochen der Extremitäten samt Schulter und Becken. *Zeitschr. f. Morphol. u. Anthropol.*, xxv, 1-90.
- NOBACK, G. J. 1922. Simple methods of correlating crown-rump and crown-heel lengths of the human fetus. *Anatom. Rec.*, xxiii, 241-244.
- PEARSON, K. 1900. Data for the problem of evolution in man. III. On the magnitude of certain coefficients of correlation in man. *Proceed. Roy. Soc., London*, lxvi, 23-32.
- PETER, K. 1920. Die Zweckmässigkeit in der Entwicklungsgeschichte. Berlin.
- PFITZNER, W. 1899. Social-anthropologische Studien. I. Der Einfluss des Lebensalters auf die anthropologischen Charaktere. *Zeitschr. f. Morphol. u. Anthropol.*, i, 325-377.
- POCOCK, R. I. 1926. The external characters of the catarrhine monkeys and apes. *Proceed. Zoolog. Soc., London*, 1925, part IV, 1479-1579.
- PORTER, W. T. 1894. The growth of St. Louis children. *Transact., Acad. Sci., St. Louis*, vi, No. 12.
- PREYER, W. 1885. *Specielle Physiologie des Embryo*. Leipzig.
- REICHER, M. 1923. The development of the growth and proportions of human fetuses. *Arch. Nauk Antropol.*, ii, No. 5 (in Polish with English abstract).
- . 1925. Croissance des membres de l'homme avant la naissance. *Travaux de la Soc. des Sciences mathém. et nat.*, ii (in Polish with French abstract).
- RETZIUS, G. 1904. Zur Kenntnis der Entwicklung der Körperformen des Menschen während der fötalen Lebensstufen. *Biolog. Untersuch.*, N. F., xi, 33-76.
- ROBERTS, R. C. 1906. On the uniform lineal growth of the human foetus. *The Lancet*, clxx, 1, 295.
- RODES, C. B. 1906. The thoracic index in the negro. *Zeitschr. f. Morphol. u. Anthropol.*, ix, 103-117.
- RÖSE, C. 1905. Beiträge zur europäischen Rassenkunde. *Arch. f. Rassenbiol.*, ii, 689-798.
- RÜDINGER, 1877. Vorläufige Mitteilungen über die Unterschiede der Grosshirnwindungen nach dem Geschlecht beim Fötus und Neugeborenen mit Berücksichtigung der angeborenen Brachycephalie und Dolichocephalie. *Beiträge z. Anthropol. u. Urgesch. Bayerns*, i, 286-307.

- SARASIN, P., and F. SARASIN. 1892-93. Die Weddas von Ceylon und die sie umgebenden Völkerschaften. Wiesbaden.
- SCAMMON, R. E., and W. H. RUCKER, 1921. Changes in the form and dimensions of the chest at birth and in the neonatal period. *Amer. J. of Diseases of Children*, xxi, 552-564.
- SCAMMON, R. E. and L. A. CALKINS. 1923. Simple empirical formulae for expressing the lineal growth of the human fetus. *Proc. Soc. Exp. Biol. and Med.*, xx, 353-356.
- SCHAEFFER, O. 1893. Untersuchungen über die normale Entwicklung der Dimensions-verhältnisse des fötalen Menschenschädels, mit besonderer Berücksichtigung des Schädelgrundes und seiner Gruben. München.
- . 1896. Ueber die fötale Dolico- und Brachycephalie. *Zeitschr. f. Geburtsh. u. Gynäkol.*, xxv, 19-59.
- SCHLAGINHAUFEN, O. 1911. Die Körpermasse und der äussere Habitus eines jungen weiblichen Schimpansen. *Abhdl. u. Ber. d. K. Zoolog. u. Anthropol.-Ethnogr. Museums, Dresden*, xi, No. 4.
- SCHULTZ, A. H. 1918. Relation of the external nose to the bony nose and nasal cartilages in whites and negroes. *Amer. J. Phys. Anthropol.*, i, 329-338.
- . 1919. Changes in fetuses due to formalin preservation. *Amer. J. Phys. Anthropol.*, ii, 35-41.
- . 1920. The development of the external nose in whites and negroes. *Contribut. to Embryol.*, ix, 173-190. Carnegie Instit. Washington, Publ. No. 272.
- . 1921 (a). Sex incidence in abortions. *Contribut. to Embryol.*, xii, 177-191. Carnegie Instit. Washington, Publ. No. 275.
- . 1921 (b). Fetuses of the Guiana Howling monkey. *Zoologica*, iii, 243-261.
- . 1922. Das fötale Wachstum des Menschen. *Verhdl. Schweizer. Naturforsch. Gesell., Bern*, Part 2, 295-299.
- . 1923 (a). Comparison of white and negro fetuses. *Eugenics in Race and State*; Second Internat. Congr. of Eugenics, ii, plates 11 and 12. Baltimore.
- . 1923 (b). Fetal growth in man. *Amer. J. Phys. Anthropol.*, vi, 389-399.
- . 1924 (a). Observations on Colobus fetuses. *Bull. Amer. Mus. Nat. Hist.*, xlix, 443-457.
- . 1924 (b). Growth studies on primates bearing upon man's evolution. *Amer. J. Phys. Anthropol.*, vii, 149-164.
- . 1925 (a). Embryological evidence of the evolution of man. *Journ. Washington Acad. of Sciences*, xv, 247-263.
- SHULTZ, A. H. 1925 (b). Studies on the evolution of human teeth. *Dental Cosmos*, lxvii, 935-947, 1053-1063.
- . 1926 (a). Anthropological studies on Nicaraguan Indians. *Amer. J. Phys. Anthropol.*, ix, 65-80.
- . 1926 (b). Studies on the variability of platyrrhine monkeys. *Amer. J. of Mammalogy*, vii, (in press).
- . 1926 (c). Variations in man and their evolutionary significance. *Amer. Naturalist*, lx, 297-323.
- SCHWALBE, G. 1899. Studien über Pithecanthropus erectus Dubois. *Zeitschr. f. Morphol. u. Anthropol.*, i, 16-240.
- . 1911. Ueber die Richtung der Haare bei den Affenembryonen. *Studien über Entwicklungsgesch. d. Tiere*, H. 15. Menschenaffen. Wiesbaden.
- SCHWERTZ, F. 1910. Untersuchungen über das Wachstum des Menschen. *Arch. f. Anthropol.*, N. F., x, 1-38.
- SELENKA, E. 1892. Affen Ostindiens. *Studien über Entwicklungsgesch. d. Tiere*, H. 5. (plates 36, 39, and 40). Wiesbaden.
- . 1899-1900. Entwicklung des Gibbon (Hylobates und Siamanga). *Studien über Entwicklung u. Schädelbau*. Liefer. 2 & 3.
- . 1903. Zur vergleichenden Keimesgeschichte der Primaten. *Studien über Entwicklung u. Schädelbau*. Liefer. 5.
- SERRANO. 1895. *Tratado d'osteologia humana*. II. Lisboa.
- SONNTAG, C. F. 1924. On the anatomy, physiology, and pathology of the orang-outan. *Proceed. Zoolog. Soc., London*, Part II, 349-450.
- SOULARUE, G. M. 1899. Recherches sur les dimensions des os et des proportions squelettiques de l'homme dans les différentes races. *Bull. Soc. Anthropol.*, Paris, 4^e sér., x, 328-381.
- STRATZ, C. H. 1909 (a). Wachstum und Proportionen des Fötus. *Zeitschr. f. Geburtsl. u. Gynäkol.*, lxxv, 36.
- . 1909 (b). Wachstum und Proportionen des Menschen vor und nach der Geburt. *Arch. f. Anthropol.*, N. F., viii, 287-297.
- STRAUS, W. L. JR. 1927. The growth of the human foot and its evolutionary significance. *Contribut. to Embryol.*, Carnegie Instit. Washington, Publ. (in press).
- STREETER, G. L. 1920. Weight, sitting height, head size, foot length, and menstrual age of the human embryo. *Contribut. to Embryol.*, xi, 143-170. Carnegie Instit. Washington, Publ. No. 274.

- TODD, T. W. 1912. The descent of the shoulder after birth. Its significance in the production of pressure symptoms on the lowest brachial trunk. *Anatom. Anz.*, xli, 385-397.
- . 1925. The reliability of measurements based upon subcutaneous bony points. *Amer. J. Phys. Anthrop.*, viii, 275-279.
- TOLDT, C. 1879. Altersbestimmungen menschlicher Embryonen. *Prager mediz. Wochenschr.*
- . 1903. Ueber die äussere Körperform zweier verschieden grosser Embryonen von *Macacus cynomolgus* L. *Arch. f. Anthrop.*, xxviii, 277-287.
- TRINCHESE, S. 1870. Descrizione di un feto di Orang-Utan. *Annali del Museo civico di storia naturale di Genova*, i, 9-46.
- TSCHEPOURKOVSKY, E. 1911. Anthropologische Studien. *Arch. f. Anthrop.*, N. F., x, 151-186.
- TSCHULOK, S. 1922. Deszendenzlehre. Ein Lehrbuch auf historisch-kritischer Grundlage. Jena.
- TUTTLE, L. 1908. The relation between weight and age in the fetus. *J. Amer. Med. Assoc.*, li, 919.
- VERNON, H. M. 1903. Variation in Animals and Plants. *Internat. Scient. Ser.*, lxxxviii, London.
- WEBER, M. 1896. Vorstudien über das Hirngewicht der Säugetiere. *Festschr. f. C. Gegenbaur*, iii, Leipzig.
- WEISSENBERG, S. 1895. Ueber die Formen der Hand und des Fusses. *Zeitschr. f. Ethnologie*, xxvii, 82-111.
- . 1911. Das Wachstum des Menschen nach Alter, Geschlecht und Rasse. *Studien u. Forsch. z. Menschen- u. Völkerk.*, viii. Stuttgart.
- WELCKER, H. 1862. Untersuchungen über Wachstum und Bau des menschlichen Schädels. 1st part. Leipzig.
- WIEDERSHEIM, R. 1901. Beiträge zur Kenntnis der äusseren Nase von *Semnopithecus nasicus*. *Zeitschr. f. Morphol. u. Anthrop.*, viii, 300-350.
- . 1908. Der Bau des Menschen als Zeugnis für seine Vergangenheit. Tübingen.
- WOLF, J. 1925. Ein Beitrag zur Lage- und Formentwicklung des embryonalen menschlichen Schulterblattes. *Zeitschr. f. Anat. u. Entwicklungsgesch.* lxxvii, 245-248.
- WOODBURY, R. M. 1921. Statures and weights of children under six years of age. U. S. Dep. of labor, Children's Bureau, Publ. No. 87. Washington.
- WOOD JONES, F. 1920. The Principles of Anatomy as Seen in the Hand. London.
- WORONJEW, W. W. 1901. Das äussere Ohr des Menschen. *Arb. d. anthrop. Abteil. d. K. Gesell. d. Freunde d. Naturwiss., Anthrop. u. Ethnol.*, Moskau, xx (Russian). Abstract in *Arch. f. Anthrop.*, xxviii, 388.
- ZANGEMEISTER, W. 1911. Die Altersbestimmung des Foetus nach graphischer Methode. *Zeitschr. f. Geburtsch. u. Gynäkol.*, lxix, 127-142.
- ZEISING, A. 1854. Ueber die Metamorphosen in den Verhältnissen der menschlichen Gestalt von der Geburt bis zur Vollendung des Längenwachstums. *Abhandl. d. Bonner Akad.*, xxvi.





THE BIOLOGY OF THE TERMITE CASTES

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I. INTRODUCTION

THE question of polymorphism or the evolution of the castes of the social insects such as bees, ants and termites or "white ants" has ever been a troublesome stumbling block to the exponents of the various theories of the evolution of species. Charles Darwin frankly admits in his "Origin of Species" that the question as to how the characters of the sterile workers and soldiers secure representation in the germ cells of the species cannot be satisfactorily explained by the theory which he advocated. There is no doubt but that if the phylogenetic mode of origin of these castes in termites could be determined, this would have a most important bearing on the theories of evolution.

Several methods of attacking the problem may be presented, such as, (1) by the study of fossil insects from the Eocene, where termites first appeared, up to the present time, the Pleistocene; or (2) by taxonomic and morphological studies of termites and their phylogeny; or (3) by biological breeding experiments to determine the type of progeny developing from the various types of reproductive forms within the species, from interbreeding these, and from hybridization.

In undertaking this important problem, involving fundamental biological laws of broad application the aid of many biologists must be enlisted; the subject is too comprehensive for the present small group of enthusiastic students, who are, how-

ever, doing all that it is possible for them to do.

The gross anatomy of the digestive systems of termites containing symbiotic intestinal protozoa (Mastotermitidae, Kalotermitidae and Rhinotermitidae) should be compared with termites normally without such intestinal protozoa (Termitidae). More thorough studies should be made of the remarkable post-adult growth and metabolism of the physogastric queens. But little is known of the glandular (both salivary and exudatory), muscular, reproductive and respiratory systems or of the morphology and operation of the sense organs, and studies of them should yield important data relating to the biology of termites. Additional histological studies, such as those made of the brains, eyes and sex organs in 1916 by the late Dr. C. B. Thompson of Wellesley College, are needed.

In cytology, further studies of the chromosomes, such as made by Dr. Alice Boring of Wellesley College, and of the germ cells are necessary before any positive results can be obtained in the genetics of termites. Cytological studies of the eggs in connection with experimentation are needed in all social insects with caste systems. Studies in embryology and physiology are necessary, as well as of the special foods leading to post-adult growth or physogastry of the termites and of some of their insect guests or "inquilines."

The genetics of termites and the study of termite breeding offer a field of special

interest and importance since principles of broad application are involved.

Behavior, biology, ecology, and geographical distribution and relationships studied in connection with intestinal protozoa should yield important results. No careful studies have been made of the ontogeny of the castes, as to the exact numbers of ecdyses or molts of the nymph to adult, and the external and internal metabolic changes incident to each instar; nor of the manner of colonization by the different reproductive forms.

Historical surveys of the work that has already been done in this group may be found in several of the papers listed among the references. The late Dr. B. Grassi of Italy was one of the pioneers in the study of both termites and their intestinal protozoa, although the writer cannot agree with many of his conclusions.

II. TERMITES OR WHITE ANTS

Termites live permanently together in more or less fixed, organized communities or large colonies, as do the other "social insects," such as ants, bees and wasps. Soldiers and workers are included in the parent colony, in addition to the sexual adults and young; that is, there is a caste system, with a more or less closely adhered-to division of labor in the termite community; every effort is for the common benefit of all castes.

While grouped with the social insects, termites are systematically classified in a lower or more primitive order; there are also marked differences in the biology of termites from that of the other social insects.

Termites or "white ants" constitute the separate order Isoptera, of which there are four families, containing approximately one hundred and forty-two genera or subgenera and in round numbers about 1,500 known or described species. These

insects occur in all the warmer regions of the world, but reach their greatest numbers and the height of their development in the tropics. In the United States 42 species of termites occur, representing 11 genera or subgenera and the three families, Kalotermitidae, Rhinotermitidae and Termitidae.

Termites are insects of great economic importance, since the principal food of some of the castes of all termites is cellulose. In obtaining this cellulose in its varied forms they directly injure and destroy both living vegetation, crops, and buildings as well as material stored therein. Termites are among the few forest insects that are able to live in and on both decayed and living plant tissue. Often material is also indirectly damaged when it lies in the path of termites as they search for food. Termites do millions of dollars worth of damage annually; such losses occur in both the tropics and in the temperate regions of the world.

While not dominant insects like the ants which *over-run* the tropics, termites by their hidden or subterranean activities silently, secretly and ceaselessly work their insidious damage and are able to *under-run* some tropical countries. A recognition of the powers for destruction or aggressiveness of tropical termites may be seen in such specific names as *atrox*, *bellicosus*, *destructor*, *devastans*, *dirus*, *fatalis*, *ferox*, *militaris*, *molestus*, *mordax*, *pugnax*, etc.

It is especially fortunate that many termite species and genera have received good descriptive names, based on characteristics or habits; i.e., "*flavipes*" (yellow legs), "*lucifugus*," (light shunning), "*perarmatus*" (thoroughly armed), etc. "*Kaloterмес*" (beautiful termites) is an especially suitable name for a genus rich in beautiful and striking species. "White ants," "wood lice," "comegen," and

"cupim" (America), "weisse Ameisen," and "fourmis blanches" (Europe), and "anay" in the Philippines are some of the vernacular names (see Hagen, 1855).

Unlike beetles and butterflies, termites are not in general beautiful, and when preserved do not make such a gorgeous display and do not attract amateur collectors. Furthermore, unlike the true ants, they are soft-bodied and very fragile when dry, hence pinned specimens are liable to become shrunken and broken. Nevertheless, while these insects do not attract the attention of general collectors, the study of termites as social insects is fascinating. There are many unsolved problems in their biology and ecology that are of great general interest, moreover, studies of termites can be conducted in this country, as well as in the tropics.



FIG 1 MACROPTEROUS, WINGED, SEXUAL ADULT OF *Reticulitermes flavipes* BANKS (FAMILY RHINOTERMITIDAE) —ONE OF THE SUBTERRANEAN TERMITES OF SOUTHEASTERN UNITED STATES

III. THE TERMITE CASTES

Termites are among those insects in which the metamorphosis is incomplete; there is a direct development from egg, to nymph to adult; termites are always superficially "ant-like" in form. No long resting or

pupal stage occurs as among insects with a complete metamorphosis; however, quiescent molting stages of relatively short duration occur at each ecdysis. Being in the group of the social insects, there are various different forms or castes within the same species.

In addition to the sexual, winged (macropterous), colonizing, reproductive adults (fig. 1), and its dealated form, there are brachypterous and apterous repro-

ductive adults (fig. 2) of both sexes and also a series of "intermediate" forms ranging from macropterous to apterous adults. Sterile as well as sexual forms exist, and are called workers and soldiers (fig. 3); each caste consists of individuals of both sexes, but the workers and soldiers normally possess non-functional sex organs; there may be two different types of workers and three different types of soldiers of the same species of termite.



FIG 2 EGG LAYING, POST ADULT FEMALES OR QUEENS OF THE MOST COMMON, SUBTERRANEAN TERMITE OF EASTERN UNITED STATES, *Reticulitermes flavipes* KOLLAR

(a) Queen with wing stubs (dealated) developed from the macropterous colonizing form, (b) brachypterous form, (c) apterous form, these queens have corresponding males and the types interbreed in nature

The evolution and biology of these castes among termites have always been problems of great general interest to biologists. There are two views as to the origin of the castes, both based on observation and experiment. According to the first view, held by Grassi (1893) and later by Jucci (1920 and 1924), the young are all alike and undifferentiated at the time of hatching, but differentiate into the various adult castes through the influence of external factors of the immediate environment such as food, or because of castration by intestinal proto-

zoan parasites, or as a result of the care received from the workers, etc.

Adherents to the second view, are the late Dr. C. B. Thompson of Wellesley College (1917-1922), Dr. T. E. Snyder (1913-1926), the distinguished Swiss entomologist Dr. E. Bugnion, the noted British entomologist Dr. A. D. Inms, as well as many others; they claim that the young are *not* all alike at the time of

soldiers from the eggs were erroneous, but other data presented by him confirm the ontogenetic origin of the termite castes.

It is believed by the writer that the histological studies conducted by Miss Thompson have proved that the ontogenetic origin of the termite castes is due to *intrinsic* causes of germinal origin and *not* to *extrinsic* stimuli which for many years have been credited with formative—



FIG. 3. (a) WORKERS AND (b) SOLDIERS OF *Reticulitermes flavipes* KOLLAR, THE COMMON SUBTERRANEAN TERMITE OF THE FAMILY RENOITERMITIDAE OF EASTERN UNITED STATES

hatching, but the castes are hereditary. Some, if not all, of the different castes are distinguishable from the beginning and the castes are therefore predetermined in the egg or embryo by intrinsic factors.

Bugnion (1913-1920) was the first modern biologist to present evidence that the castes of termites are determined in the egg. His observations on the hatching of externally, maturely developed

indeed almost creative—powers. Which of these views is correct? Or are they both in part true?

The fertile and sterile types even as nymphs are internally differentiated at the time of hatching, and very early in their postembryonic development all of the adult castes may be distinguished. These facts disprove the older hypothesis that castes may be determined or changed

by external means. A natural explanation is that the castes have originated by segregation from a heterozygous parent form. Preliminary studies by Boring reveal no visible differences in the chromosomes of the various castes.

In collecting termites for study, every effort has been made to obtain as many of the forms or castes as possible; specific descriptions and identifications are based either on the winged or soldier caste, and it is essential to obtain winged adults or soldiers. However, some specific as well as family and generic characters occur in the worker caste in certain genera; the worker caste should receive further study. Species in most genera in the family Kalotermitidae have no worker caste, the duties of the workers being performed by the young or nymphs, whereas in the genus *Anoplotermes* Fritz Müller in the family Termitidae, the soldier caste is lacking. It is necessary to collect the winged forms or the queens in order to make specific identifications in the genus *Anoplotermes*.

IV. THE TAXONOMY OR CLASSIFICATION OF TERMITES

The most complete and satisfactory classification of termites, based on world collections, is that of the distinguished Swedish entomologist Holmgren (1909-1913); this most nearly approaches a natural system. While this classification is accepted in general by American workers in this group, certain minor phases are rejected, and others are temporarily accepted with reservation, as for instance, the validity of certain subgenera, especially of *Kalotermes* and *Nasutitermes*.

According to Holmgren, there are in the order Isoptera four families, ranging in degrees of specialization from the Mastotermitidae and Kalotermitidae through the Rhinotermitidae to the most highly specialized family the Termitidae.

Winged adults of the living species of the Mastotermitidae (there being one living and four fossil species) have large anal and postanal fields in the hind wings, the humeral suture or point of breakage is absent in the hind wing, the fore-wing scale is large; there are 5 tarsal joints; the fontanelle is absent; ocelli are present; the pulvillus between the apical claws on the tarsi of the legs is present; the pronotum is flat. Both soldiers and workers are present. Macropterous and apterous reproductive forms occur in colonies.

In the winged adults of the species of the Kalotermitidae, the postanal field and enlarged anal fields are lacking in the hind wing, but in this wing there are sometimes rudimentary anal branches, the humeral suture is incomplete (as in *Termopsis*) or complete, the fore-wing scale is large (small in *Hodotermes*), the wings are usually reticulated; 5 to 4 tarsal joints; fontanelle absent; ocelli present (or absent in *Archotermopsis*, *Termopsis*, *Hodotermes* and *Porotermes*—"false ocelli" occur in *Hodotermes*); pulvillus usually present (normally absent in *Hodotermes* and *Porotermes*). Soldiers are present, but workers are absent, except in *Hodotermes*. Macropterous, brachypterous, and apterous reproductive forms occur, the prevalence of a certain type varying with the genus.

Holmgren has established the four subfamilies Termopsinae (*Archotermopsis*, *Hodotermopsis* and *Termopsis*), Hodotermitinae (*Hodotermes*, *Macrobodotermes* and *Anacanthotermes*), Stolotermitinae (*Stolotermes*), and Kalotermitinae (*Porotermes* and *Kalotermes* l.s.).

The genus *Termopsis* in the subfamily Termopsinae is more primitive than the genus *Kalotermes* of the family Kalotermitidae, because the contained species are not so well defined in *Termopsis* as in *Kalotermes* of the subfamily Kalotermitinae. In the latter genus, some species are very distinct and the species are more numerous than in

Termopsis. In species of *Kaloterme*s there is a reduction in the number of antennal segments. However, ocelli are present in *Kaloterme*s but absent in *Archoterme*opsis, *Termopsis* and *Poroterme*s. The presence of ocelli is a primitive character. Workers are absent in *Archoterme*opsis and *Termopsis*.

In the subfamily Hodotermitinae, species in the genus *Hodoterme*s (l.s.) are grass or leaf-cutting termites and in their structure and pigmentation, they also show considerable progressive development; ocelli are absent but "false ocelli" are present. While they nest in subterranean cavities and galleries, they are termed "wander-termites," since both the workers and soldiers of some of the species are darkly pigmented, have faceted eyes and long legs, and forage above the ground during the day exposed to the sunlight, as do some of the more highly specialized Termitidae. In the subgenus *Macrobodoterme*s, soldiers are never (or seldom) seen outside of their burrows during the day. In *Hodoterme*s (l.s.) the pronotum is sellate or saddle-shaped—a specialized progressive character. There are no secondary sexual characters to be seen in the apex of the abdomen; both sexes possess styli. In *Macrobodoterme*s, however, abdominal styli are atrophied or missing, indicating a progressive reduction.

The presence of this highly specialized worker caste gives some credence to the view that *Hodoterme*s might be classified in a distinct family the Hodotermitidae, possibly related to the intermediate Rhinotermitidae; ocelli are sometimes lacking in species of *Leucoterme*s in the latter family. Furthermore, in the genus *Serriterme*s in the Rhinotermitidae, there is also a highly specialized worker caste and these termites are foraging in habit. Preliminary studies of intestinal protozoa by Dr. Harold Kirby, Jr., of Yale University rather indicate such a relationship between *Hodo-*

termes and the Rhinotermitidae. However, all phases of the subject should be much more thoroughly studied before any such radical change could be accepted.

In the primitive genus *Kaloterme*s of the subfamily Kalotermitinae, now classified as closely related to the genera *Termopsis* and *Hodoterme*s, ocelli are present—a primitive character; there is also color in the reduced eyes in the soldier in some species. Hagen in 1858 considered *Kaloterme*s to be the most primitive genus known. The pronotum is arched and of the blattid type (Fuller, 1924). No worker occurs in any of the species in this subfamily.

In *Poroterme*s, however, in the same subfamily with *Kaloterme*s, ocelli are absent. *Poroterme*s was formerly considered to be a subgenus of *Hodoterme*s, since the subcostal vein in the wing is absent or rudimentary. According to Kirby, the intestinal protozoa of *Poroterme*s appear to be related to those of *Hodoterme*s and the Rhinotermitidae as well as to the flagellates of *Kaloterme*s.

In the intermediate family Rhinotermitidae, the fontanelle, with few exceptions, is present in glandular form; the fore-wing scale is large (except in *Psammoterme*s), the wings are usually reticulate, the reticulation of the wing membrane becomes rudimentary and almost disappears in the higher subfamilies; the pulvillus is absent. The pronotum is subcordate to slightly saddle-shaped. In *Serriterme*s both the soldiers and workers are highly specialized as "wander" termites. Macropterous, brachypterous and apterous reproductive adults occur in colonies; both of the latter forms are common, but brachypterous adults have become the more highly specialized.

Six subfamilies of the family Rhinotermitidae have been established by Holmgren.

The most highly specialized termites are in the family Termitidae; the fontanelle always has a plate-like structure; the fore-wing scale is small; the wings are not strongly reticulate; the pulvillus is absent. Workers and soldier are present, except in *Anoplotermes* where the soldier is lacking. The pronotum is sellate, and specialized thoracic spines occur on both the soldiers and workers of certain "wander" termites (*Syntermes* and *Acanthotermes*). Macropterous and brachypterous reproductive adults occur, but the apterous form is apparently lacking or, if it occurs, is very rare; its disappearance is a progressive development from the lower termites.

Holmgren has established four subfamilies in the family Termitidae. The Termitinae (including the *Termes* or fungus-growing group); the *Syntermes* group, which includes foraging and harvesting termites (in *Syntermes* and *Speculitermes*); *Amisotermes* (including the Australian termite with "compass" mound nests); and the *Miro-Capritermes* group; in the latter group are those termites whose soldiers have asymmetrical, non-biting mandibles. The Microcerotermitinae, Pseudomicrotermitinae and Foraminitermitinae are the other subfamilies.

V. THE PHYLOGENY OF TERMITES AS EVIDENCED BY PALAEONTOLOGY, TAXONOMY AND BIOLOGY

Although termites have a close systematic relationship with the roaches or Blattidae, they are much younger geologically, and therefore more recently evolved. No fossil termites are known from the Mesozoic Age, but termites may have existed in the Cretaceous period; they occur in all deposits from the Lower Tertiary on.

As Holmgren concludes, both termites and roaches are probably offshoots of a more primitive group. None of the fossil

termites are more generalized or more primitive than living termites. Indeed, a living species of the genus *Mastotermes* Froggatt of Australia is the most primitive (Froggatt, 1895-1923); this termite has a wing structure similar to the roaches, remarkably developed reproductive organs in the female, and recently (1925) Hill has discovered that the egg mass is similar to the oötheca of the roaches indicating at least common ancestry. However, three species described as *Mastotermes* by Von Rosen (1913) have also been found as fossils in the Tertiaries of Great Britain and one in Croatia. Nevertheless, in prehistoric times there was naturally a greater prevalence of primitive termites than at present.

The wings of the large and most primitive living termite, *Mastotermes darwiniensis* Froggatt in the family Mastotermitidae, the lowest termites, have a large anal field, as in roaches. This most primitive termite (in the *lowest* family) has a soldier much more specialized than would be expected; this soldier and the worker of the same species were erroneously described by Froggatt, after he had already described the winged adult, as *Termes errabundus* and placed in the family Termitidae, which contains the *highest* termites. Even in this primitive species the worker caste is present, although this caste is usually lacking in the next higher family, the Kalotermitidae.

According to Caudell (Snyder, 1924), in the wings of certain roaches a break often occurs following in general the anal sulcus at the base resembling the humeral suture of termites, where the wing breaks off after flight; in primitive termites this suture is also often poorly defined. In the biology of termites and roaches there are other similarities based on homologous structures, but termites have become more highly specialized and have become social

in habit, with a well-developed caste system. Even the most primitive termite *Mastotermes darwiniensis* is a very destructive wood borer, with diffused nests containing large numbers of individuals.

Roaches seldom are found boring in sound wood; the logs that they inhabit are usually decayed, and they utilize the burrows of wood-boring insects, or live under the logs, or between the bark and wood. However, a large, brown, wingless roach (*Cryptocercus punctulatus* Scudder) lives by burrowing in fairly solid wood in partly decayed chestnut and coniferous (pine and fir) logs in the Appalachian Mountain region and on the Pacific Coast.

According to Kirby, domesticated roaches contain the only Hypermastigata flagellate not found in termites, a flagellate related to those of some of the Kalotermitinae. It would be extremely interesting to study the protozoa of the roach *Cryptocercus* from its native habitat, since this insect apparently eats the wood through which it burrows. The wood may be so decayed, however as to be broken down already by wood-destroying fungi.

Some of the primitive termites (*Archotermopsis* and *Termopsis*) normally inhabit the wood of conifers but not that of Angiosperms, which are geologically more recent plants. This, however, may be due to the fact that the common habitat of these termites and conifers is in a colder climate than is usual for most termites, although these termites are among the oldest (geologically) that have been found as fossils.

The young or nymphs of certain species of *Kalotermites*, *Prorhinotermes* and *Coptotermes*, possess wing pads on the pronotum; these later disappear in the development of the nymph to the adult. The appearance of transitory, vestigial wings so early in the ontogeny of termites is an-

other indication of the recapitulation of the phylogeny of termites, since (Imms, 1919 and Fuller, 1924) similar alar structures also appear on fossil orthopterous insects (Carboniferous). Both the Isoptera and Orthoptera were derived from a common ancestor.

Species of *Zorotypus* of the southern United States in the order Zoraptera Silvestri are gregarious and have both apterous and winged reproductive forms as in the most primitive termite (*Mastotermes*); the latter forms lose their wings after flight in a manner similar to that in the lower termites, the point of breakage being poorly defined; there is also a tendency to variation in wing venation among individuals as in termites; the reproductive organs are well-developed. No worker or soldier castes exist in *Zorotypus*, but it is believed by the writer that these insects are closely related to termites and that *Zorotypus* is at the dawn of social life. The habitats of these insects are in situations similar to those where termites live and they superficially resemble young termites, but move much more rapidly. It is not known whether intestinal protozoa occur in species of *Zorotypus*.

As Crampton has shown (1920), in *Mastotermes* there is a remarkable development in the alate female of a fully formed ovipositor. The external genitalia are unlike those of any other termites (where they are reduced) resembling in general the arrangement in the roaches. This is an indication that the primitive termite *Mastotermes* is most nearly related to ancestors non-social in habit.

VI. THE PHYLOGENY OF THE TERMITE CASTES AS EVIDENCED IN THEIR ONTOGENY

While there are no authentic paleontological records of termites before the Tertiary, Wheeler has stated (1923) that

"in all probability the termites, like the ants, reached their complete structural and social development in the late Cretaceous or early Tertiary and have since undergone very little modification."

It is believed that the ancestral termite, like the ancestral roach, consisted of merely winged males and females. The only fossil forms of the most primitive termites found have been winged. The prototype of both termites and roaches was also probably winged, although insects originated from a worm-like ancestor.

The records written by fossil termites are at best very imperfect. While it has not been proved that wingless termite castes occurred in the Tertiary period, they doubtless occurred and were probably evolved during the late Cretaceous period. Polymorphism among the social insects may not have been as highly developed as at present, especially in the case of the reproductive forms, but it can not be stated that the sterile castes and colony or social habits developed since Tertiary times because of lack of fossil forms. Due to their habits, such sterile forms would be less likely to be preserved as fossils. Both mandibulate soldiers and nasuti in clearly differentiated fossil form have been found embedded in gum copal from the Pleistocene period of comparatively recent formation.

It does not seem probable that the elaborate polymorphism that occurs today existed among the reproductive castes in termites during the Tertiary period; it is believed that a greater polymorphism probably has come about since the Tertiary.

At least two other dissimilar or distinct, sexual, colonizing adults, as well as a series of intermediate forms have evolved from the original macropterous or winged form. Both brachypterous and apterous reproductive adults occur in some of the

most primitive or lowest living termites. Apterous forms are common in *Mastotermes*, *Termopsis*, *Hodotermes*, and more rare in *Kalotermes*, as well as common in the next higher termites, the Rhinotermitidae; however, brachypterous reproductive adults do not occur in *Mastotermes*.

Fuller of South Africa has sent to the writer specimens of a yellowish, apterous caste, larger than the worker that is found with species of *Macrobodotermes* Fuller; this caste has black pigmented eyes and may be a third form (apterous) reproductive adult. Also an apterous queen of *Hodotermes* (*Anacanthotermes*) *abnigerianus* Jacobs. of Turkestan is figured by Vasiljev (*Revue Russe d'Entomologie* XI, 1911, pp. 235-245); the color of the head of this apterous form is brown and the eyes are black-brown.

Brachypterous reproductive forms while absent in *Mastotermes* are common in *Termopsis*, but are rare in *Kalotermes*, again becoming common in many of the Rhinotermitidae.

Among the highest termites (Termitidae), while brachypterous adults commonly occur (in *Armitermes*, *Nasutitermes* and *Microcerotermes*), apterous forms are apparently lacking.

These three reproductive adults develop from nymphal prototypes similar to the adult (unlike in the case of the soldier caste). Presumably, a direct development is also the case in the "intermediate" reproductive forms.

While both the worker and soldier castes occur in the most primitive termites (*Mastotermes* and *Hodotermes*), the worker is absent in other primitive groups (*Archotermopsis*, *Termopsis*, *Kalotermes* and *Porotermes*) but occurs in all the intermediate and in the highest termites. Hence, there is some doubt as to the evolution of the worker and soldier castes and as to which was derived first.

Fuller believes that the very highly specialized worker caste present in *Hodotermes* has been lost in *Termitopsis* and *Kalotermites* as the soldier has been lost in *Anoplotermes*, one of the higher termites.

Soldiers of primitive termites are of only one type (are monomorphic); in the intermediate termites they become impressively dimorphic; and in the higher termites trimorphic; but among the most specialized termites they again become monomorphic.

Among some of the species of *Termitopsis* and *Kalotermites*, a small proportion of the soldiers in the colonies are commonly found to have wing pads or vestigial wings. Indeed, in a very primitive and the largest known species of *Kalotermites*, namely, *K. occidentis*, described in 1853 from the soldier caste by Walker from the West Coast of Central America, and also occurring in Arizona and Lower California, every specimen of soldier which has been found in the colonies has vestiges of wings or rudimentary wing pads. It is believed that this is a primitive or ancestral character; or a reversion to the condition when all the present "social insects" were merely male and female winged forms with no sterile worker or soldier castes.

Holmgren established a new subgenus (*Pterotermes*) for this termite (*occidentis*), which is merely a primitive *Kalotermites*. The reduced eye spots of the soldier have a black color, as is the case in several other species of *Kalotermites*; the eyes are not, however, to be compared with the well developed pigmented eyes of the soldier of *Hodotermes*. Winged adults of *K. occidentis* recently have been found and described by Banks (1920).

No workers with wing pads ever have been found among any of the termites. Furthermore, in some primitive termites (*Archotermopsis* and *Termitopsis*) there are indications that female soldiers are fertile

and able to lay eggs, a reversion to the ancestral state when only male and female adults were present. In these two genera there are also external secondary sex characters in the soldier caste. Although there is an "ergatoid" or worker-like, apterous reproductive form in termite colonies, no potential or egg-laying workers ever have been found.

Does the ontogeny of the soldier caste, which develops from a very different, worker-like prototype, recapitulate the phylogeny of the soldier caste, or did the worker caste evolve from the soldier? This latter view of the derivation of the worker caste was first advocated as a theory by Emerson of the University of Pittsburgh, and was based on studies of the ontogeny of the soldier in a *Constrictotermes*.

Genetic formulae for termites would show that the broods differ not only with the age of the colony but also with the genus and species. Of the first brood in young colonies of species of *Reticulitermes* (of the intermediate family Rhinotermitidae) in the United States (a genus where both soldiers and workers occur) most are workers and a few soldiers, but *there are no sexual forms*. This is exactly the reverse of what is believed to be the phylogeny of the termite castes. The first brood of the species of *Termitopsis* of the lower family Kalotermitidae consists of nymphs of the sexual forms and of soldiers—a more proper representation of the phylogeny of the castes.

A comparison may be made of the phylogeny of the fertile and sterile termite castes, as evidenced in their ontogeny, with the phylogeny of the fertile and sterile portions of a plant. In the white, sweet-scented water lily (formerly *Castalia*) now *Nymphaea odorata*, some of the anthers have been transformed into petals; all gradations between anther and petal

may be seen in a single flower. These petals may be less important functionally than the anthers, yet each serves a purpose. The sterile soldier termites—more highly specialized than the workers—are less important functionally than the workers and both are less necessary than the fertile forms from which they have developed. They all serve needs in the colony life.

This relative ratio between the numbers of soldiers and workers in colonies of termites holds during the second year, when sexual adults are also produced in colonies of *Reticulitermes*. In old colonies, workers (in genera where present) always greatly out-number the soldiers among *all* termites, which constitute but a small proportion of the castes in the nest; large numbers of sexual adults develop to maturity each year.

Workers are much more useful and independent than are the soldiers which need to be fed by the workers and whose effectiveness in protecting the colony in some species and genera is doubtfully as great as that of the workers. In one over-specialized genus (*Anoplotermes*) among the higher termites, the soldier caste is lacking. In this genus the workers are—both as to legs and mandibles—specially modified.

Soldiers may occur in as many as three different types (are trimorphic) in some of the higher termites and are dimorphic in some of the intermediately classified termites; whereas, the workers at the most occur in only two types in the higher termites. These facts indicate a greater specialization of the soldier caste, and possibly that this caste evolved before the worker.

Winged termites in the course of their specialization have developed the complete humeral suture and have lost the strong power of flight of the lower forms;

the reticulation of the wing membrane disappears; the wings are reduced so that in the Termitidae only about the middle portion remains; and the anterior wing scale becomes markedly reduced in size. There is the usual reduction or loss of veins in the wings from the lower to simpler-veined, higher termites; the costal area is markedly reduced. The pronotum develops from a flat type to the sellate form. The shape and position of the head with relation to the pronotum changes, the progression being to a condition of reduced mobility. Abdominal cerci and styli (atrophied or missing in *Macrohodotermes*), tarsi, lateral tibial spines and the pulvillus of the legs become reduced or lost in regressive development; although long antennae and legs again appear in the "wander" termites among the Termitidae.

The reproductive forms become polymorphic from the lower to higher termites and from relatively small, active, and less dependent forms they develop to very large, inactive forms, entirely dependent (on the workers) in the higher termites. The presence of dependent queens occurs only among termites with workers present. Why do not the nymphs take the place of the workers in this rôle?

This development of the queens is correlated with progressive evolution in the building of more permanent specialized nests. Among the lower termites the more or less temporary nests are nearly always diffused, whereas in the higher, nests are more permanent, concentrated and specialized, in *Apicotermes* of the Belgian Congo reaching a utilitarian and architectural development not exceeded even by the higher insects (the Hymenoptera).

In all of the lower and intermediately classified termites, intestinal protozoa which aid in the digestion of wood are

present. But in the highest termites (the Termitidae) protozoa are few and of the type found parasitic or commensal in other insects. So far as is known they do not play a symbiotic, helpful rôle.

The common apterous reproductive form in the lowly Mastotermitidae and Kalotermitidae and intermediate Rhinotermitidae, first becomes supplemented in the Kalotermitidae by brachypterous reproductive forms, and finally the apterous form disappears in the higher Termitidae.

In some species in the intermediate family Rhinotermitidae and higher Termitidae (in *Armitimus*), the winged or macropterous forms do not appear to be the dominant reproductive type, as is usual among the lower termites. This is especially true in species of the non-subterranean, island genus *Proshinotermes* where apterous reproductive adults are most commonly found heading colonies in moist wood in wet sites, brachypterous reproductive adults do not occur in colonies. It is believed that these termites (*Proshinotermes*) are largely dispersed in drift wood—and that colonization is by division of colonies as well as by flight.

In the species *P. simplex* Hagen in Florida no nymphs with long wing pads have ever been found in colonies although these forms occur in colonies of this species in Cuba.

In *Proshinotermes molinai* Snyder of Central America, the winged adult appears to develop from a nymph with short, circular, apparently fused wing pads. So far as can be seen from a series of specimens in alcohol from Costa Rica, these wing pads become markedly inflated just before the penultimate molt, they become raised up apically from their normal flat position and a median suture appears. This is a marked departure from the normal condition in other termites where the winged adult develops

from a nymph with long, straight wing pads.

Also, in the progress from the lower to the higher termites the functional (as biting) mandibles and rudimentary frontal gland of the soldier caste show marked changes (fig. 4). In the intermediate

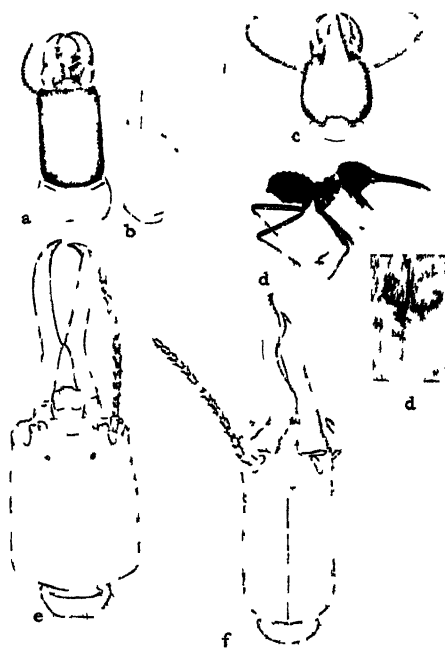


FIG. 4. VIEWS OF THE HEADS AND PRONOTA OF SOLDIER TERMITES TO SHOW REGRESSIVE DEVELOPMENT IN THE DEVELOPMENT OF THE MANDIBLES AND PROGRESSIVE DEVELOPMENT OF THE FRONTAL GLAND, FROM THE KALOTERMITIDAE (*Kiloterms*, c, d) TO THE TERMITIDAE (*Nasutitermes*, e, f).

In the family Termitidae is also seen a transitional genus *Armitimus* (c and d), where both mandibles and frontal gland are functional, also in this family, there is an overspecialization in the mandibles (*Orthognathotermes* (e) and *Nasutitermes* (f)).

family Rhinotermitidae, the frontal gland is a highly specialized organ of defense—a sticky white secretion exudes from a short tube—which is very effective against insect enemies, the labrum is also highly specialized (fig. 5), but the mandibles are functional. The pronotum changes from the ancestral flat shape to a somewhat

saddle-shaped structure,—a progressive development—; and there is progressive development in the clypeus and post-clypeus; the latter becomes markedly arched and bilobed in the higher termites.

While, in many of the higher termites, the mandibles are absent or vestigial and the frontal gland becomes even more highly specialized as a "nasus" or beak-like structure in the "nasuti," in others

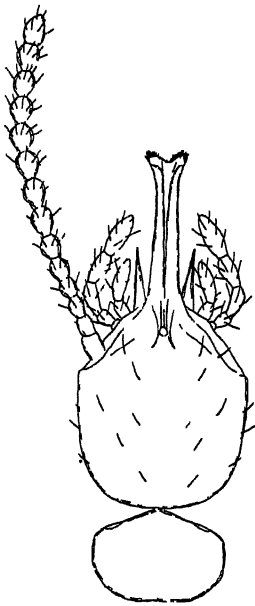


FIG. 5. HEAD AND PRONOTUM OF THE MINOR SOLDIER OF *Rhinotermes latilabrum* SNYDER TO SHOW HIGHLY SPECIALIZED LABRUM AND FRONTAL GLAND, AS WELL AS VESTIGIAL MANDIBLES

of the higher termites (*Armitermes*) both mandibles and well-developed frontal gland are functional. The condition in the genus *Armitermes* may be considered as transitional or intermediate in the progress of the evolution of this highly specialized gland and in the later reduction or regressive development of the mandibles. In some species of *Armitermes* the mandibles are more dominant than the frontal gland, in others the reverse is the case. In *Acantho-*

termes the outlet of the frontal gland is remarkably modified.

According to Holmgren (1912), in *Termes horni* and *T. ceylonicus* Wasmann the salivary glands are developed as defense glands.

In *Anoplotermes*, a genus of the higher, over-specialized termites, the soldier caste is lacking but the workers and winged adults often have very long mandibles.

Or in other over-specialized forms, the mandibles of the soldier become extended, lose the marginal teeth and do not function for biting, but are twisted and asymmetrical and are used in slipping themselves away from danger or slipping particles of dirt at invading insect enemies. The labrum also becomes progressively developed.

Morphological evolution in the soldiers of the over-specialized fungus-growing *Termes* series is generally regressive in character as is the caste system; this regression is correlated with regressive development of the nest structure. The entire system of life economy of the nest among these fungus-growing termites, which are confined to Ethiopia and Indomalaya, is most highly specialized, as evidenced by the mound nest, the huge queen imprisoned in a protected "royal cell," "nurseries" and "fungus gardens"—a sponge-like mass where special fungi are grown for food (the conidia are cropped as food by the young and are also fed to the reproductive adults). Dependence is not placed entirely upon the cellulose of wood, which has to be broken down by intestinal flagellates. Such protozoa which aid in the digestion of wood are absent in the intestines of species in the *Termes* group.

The Indian species *Hospitalitermes monaceros* Koenig has workers deeply-pigmented, with eyes well-developed and long legs, which forage above ground in the sunlight; they harvest portions of lichens for food.

Also, in the worker caste there is a progressive loss or reduction in the number of marginal teeth on the mandible, from the lower to the higher termites, and a progressive development of the frontal gland. A marked progressive development in the workers of the higher termites is the structure and marked color of the

diurnal harvesting or "wander" termites—grass or leaf-cutting species. The heads are larger than usual, the legs and antennae are often very long; the antennae have more segments than related non-wandering species—primitive characters. The intestines and salivary glands show progressive development. Among these termites are: *Hodotermes* (l.s.)—Palearctic, Ethiopian and Oriental; *Serritermes*—Neotropical; *Termes* (l.s.)—Ethiopian and Oriental; *Syntermes*—Neotropical; *Acanthotermes*—Ethiopian; *Nasutitermes* (l.s.) Neotropical and Oriental; *Speculitermes*—Neotropical and Oriental; *Drepanotermes*—Australian; all except *Hodotermes* and *Serritermes* are in the family Termitidae and lack symbiotic intestinal protozoa.

The fact that the termites of the primitive genus *Hodotermes* have a highly specialized worker caste and that they are diurnal foraging and harvesting termites—as are some of the higher termites—is difficult to explain on the basis of progressive or regressive development under the present classification of *Hodotermes*. However, in *Hodotermes* there are many primitive characters evidenced in antennae, wings, tarsi, tibial spines and cerci and in the presence of intestinal protozoa; there is no reduction to indicate progressive development. Nevertheless, in the "wander" termites among the Termitidae, there is a similar lack of reduction in antennae and legs—a regression.

VII. THE BIOLOGY OF THE TERMITE CASTES (GENERALIZED)

The "first-form" or macropterous queen produces five to seven kinds of offspring (varying with the species), one to three fertile and two to five sterile types—only one type being like itself (the parent), the others all different in structure and behavior.

There is a parallelism between termites

and Mendelian "segregants," where there is a splitting up of a complex parental hereditary material into many simpler types of offspring or segregants. Various less common, abnormal or "intermediate" reproductive adults of termites are merely other segregants.

Since we believe that it has been proved that the fertile and sterile castes are differentiated at the time of hatching and since there is no positive proof that special qualitative feeding can determine the castes (and indeed there is much evidence to disprove this) and that intestinal protozoa do not cause sterility in the neuters, but have a symbiotic relationship, the explanation of the origin of the castes due to immediate environment, such as food, can not be accepted. The castes in termites are undoubtedly blastogenic in origin. To regard them as segregants appears to be the most inclusive and plausible explanation.

At certain seasons (spring or autumn) of each year, winged, sexual, colonizing forms of both sexes appear in large numbers, in well-established colonies. Normally termites shun the light, but these forms, impelled by some irresistible impulse to leave the colony, temporarily become markedly positively phototropic. After the short, "wobbly" flight or "swarm," the dealated adults become strongly thigmotropic; they must have contact with wood or earth.

The lower termites have a longer, stronger flight and emerge from the parent colony in smaller numbers and at irregular intervals, while the more specialized termites are restricted to a few large flights annually; the humeral suture is well defined in the higher termites (Termitidae), which sometimes lose one or both pairs of wings in mid air, and then spiral to earth. The lower termites, however, are forced to pry off their wings, since the humeral

suture or line of weakness is but poorly defined.

In general, the stimuli in the termite colony are hunger, sex and fear, and in the progressive development of termites, greater specialization can be observed in food, reproduction and defense. Nevertheless, the synchronous swarming of the winged, sexual, colonizing adults is one of the rhythmic activities in the life of the termite colony which is but little understood. At a certain time on the same day thousands of winged adults will emerge from different colonies of the same species of *Reticulitermes* in logs, stumps or infested buildings (fig. 12b) in the same general locality—such as an entire town-ship or in a whole village.

Apparently, there is no *general* (of wide application) external influence, and the mature, winged adults have been in the colony for some time previous to this "swarm" (which is a colonizing and mating but *not* nuptial flight); they can be induced to fly earlier by disturbing the colony. Can one say the responsible factor is odor or some other stimulus due to developing gonads or sex cells? For these adults do not mature sexually until after the flight.

The stimulus to swarm may be humidity or rainfall in connection with the proper degree of temperature in the case of some termites which live in the earth in arid regions; or hunger in the case of species of *Reticulitermes*, where there is no food taken and the intestinal protozoa that possess enzymes for digesting cellulose—the principal food of termites—have mostly been lost during the final molt, just before the flight. Or are the winged adults forced to migrate by the workers, which with soldiers stand guard at the exits during the swarm? (fig. 12c).

In tropical countries, there is almost an element of magic attendant upon a large

termite swarm. Apertures are opened in the ground or parent colony mound and suddenly the air is alive with fluttering winged hordes. After the flight, these exit holes are closed from within by the workers and all traces of life disappear as suddenly as they appeared, the only evidence of the swarm being the discarded wings. Surely the swarm must have been an object of mystery to primitive peoples!

Normally, only *after* losing the wings are the males and females attracted to each other; they then pair off in couples, the male closely follows the female, with head close to her abdomen, stimulated and excited by a sex odor. Together they found the new colony by excavating a small cell or royal chamber in wood, under bark, or in the earth under wood lying on the ground, or in the earth. In the Kalotermitidae sex attraction is evident *before* the loss of the wings, and the males and females *sometimes* do not lose the wings until after they are established in a cell under the loose bark on trees. According to Fuller (1915), in certain African species of *Termes* the winged females settle on grass stalks and engage in a "calling attitude" to attract the males.

Coition is not by superimposition but is effected with male and female on the ground and the abdomens end to end (as in the roaches). Coition does not occur during the swarm flight, nor until the new home is established. The rate of egg-laying is at first slow in *Reticulitermes*, but more rapid in *Termopsis*; and the young parent adults feed and care for the offspring until enough of the workers or nymphs have been reared to care for the needs of the colony. Coition is continued at irregular intervals and the male continues to cohabit with the female for life.

The workers and soldiers of the first

brood that are reared in these nascent colonies are smaller than normal; this dwarf condition of the sterile castes in incipient colonies, or "nanism," is probably due to the scarcity or the character of the food and to the care when the caste system is just developing. Hence, although food both quantitatively and qualitatively may be a factor influencing size and rapidity of development, it has no rôle in determining castes.

Eggs are laid singly, except in *Mastotermes*, where they are extruded in a mass somewhat similar to the oötheca of roaches. The eggs receive the same care from the workers (are licked and tended) that is later given the young or nymphs. The development of the eggs is facilitated by temporary shifts to more favorable locations in the nest. Before hatching the eggs swell up perceptibly.

Only in the case of *Cryptotermes canisrons* Banks of southern Florida among Nearctic termites, have eggs been found in special cells outside of the royal chamber; here eggs were observed in small separate pockets in fluffy wood fibre in an infested log. In tropical termites (*Termes* group) there are special "nurseries" for the young, recently hatched nymphs.

While queens of the higher termites are larger and lay more eggs, they are normally monogamous, whereas primitive termites are more often polygamous.

The young or nymphs are always active except for relatively short quiescent or molting stages. According to Cleveland (1926) the young or nymphs contain intestinal protozoa 24 hours after hatching, showing that they are being fed by the workers or nymphs (from the ani) and are not eating wood; later they eat wood. The mature soldier, with elongate mandibles, cannot eat wood and is fed by the workers.

There is a remarkable post-adult growth

in both the male (or king) and female (or queen) as the colony increases in numbers, much more marked, of course, in the female (fig. 2). With the increase in the number of the egg tubes and actual cellular divisions and growth there is a correlated degeneration of the jaw muscles in the post-adult queens of all types. They lose much of their body color, no longer fly nor eat wood, and according to Fuller (1924), the fasciculate muscles of the thorax become degenerate. They are at this time dependent on the workers, who feed them special food from the mouth. Kings and queens may live together for as long a period as 25 years at least in artificial colonies. Old queens lose some of the segments of the antennae, tarsal joints, margins of the thorax and some body cuticle; these are possibly bitten off by workers or nymphs in their eagerness for exudate.

In well-established parent colonies of *Reticulitermes* in the eastern United States large numbers of nymphs of brachypterous and apterous reproductive forms seasonally appear each year. These forms mature at the same time as do the macropterous adults, and pass through similar molts during quiescent stages of relatively short duration, during the last of which the females (in *Reticulitermes*) lose the abdominal styli—an immature character in the female; hence they are now really an *adult caste*. In apterous reproductive adults in *Archotermopsis* and *Termopsis* the styli are *not* lost in the females. Unlike the macropterous adults, at the time of their flight the sex cells of brachypterous adults are ready to function, and they have lost their intestinal protozoa. Cleveland states that while he is not sure that these protozoa are ever entirely lost in *Termopsis*, they are at least very greatly diminished. In *Reticulitermes* protozoa disappear entirely perhaps at about the

time when the sexual organs begin to function.

Just before the flight of the winged adults, these brachypterous and apterous reproductive adults disappear from parent colonies. What happens to them? Are they killed by the workers in the parent colonies when they are not needed? Or do they migrate to form new colonies? But little is known of the biology of the brachypterous or apterous reproductive adults or castes and how they establish new colonies, which some of them do. Probably these forms migrate with workers or nymphs and soldiers for purposes of colonization through subterranean passages and are impelled by the same stimuli as are the winged colonizing adults.

Sometimes adults of both sexes in species of *Reticulitermes* engage in a short "pseudo-flight" at the same time that the winged adults are swarming. Brachypterous adults come out from the parent colony into the full sunlight and run about, or make slight short jumps or flips into the air—as do the deālated adults—and often they fall over backward in efforts to escape if disturbed. Possibly this activity is a manifestation of or a reversion to the ancestral habit of swarming, or colonization by flight.

These incompletely pigmented, brachypterous adults have the compound eyes reduced and the facets but slightly colored; with the simple eyes or ocelli they are probably able to perceive only light and direction. In *Reticulitermes* they contain (as adults) no intestinal protozoa and hence are dependent on workers for food in order to live. If in the Mastotermitidae and Kalotermitidae these brachypterous and apterous adults contain no protozoa and if workers are absent in Kalotermitinae, nymphs of the sexual adults or of the soldiers must necessarily accompany them in this migration in order to feed them.

Cleveland, however, has shown that protozoa occur in these reproductive adults when workers are not present.

Moreover, contrary to the condition in species of *Reticulitermes*, in species of *Hodotermes* (s.s.), *Anacanthotermes*, *Archotermopsis* and *Termopsis* the female adult apterous reproductive forms do *not* lose the abdominal styli in the final molt; hence there also may be differences in the manner of their colonization. These styli are absent in mature, egg-laying, macropterous queens in species of *Archotermopsis* and *Termopsis*, but are present in this same form in species of *Hodotermes*, except in *Macrobodotermes*.

Adults of the apterous reproductive forms in species of *Reticulitermes* have but little color to the body (less than in brachypterous adults) and there are but traces of eyes, whereas in *Prorehinotermes*—as in the lower Kalotermitidae, especially *Termopsis*—there is a marked color to the body and the eyes are merely reduced. Probably only the completely pigmented, winged, colonizing adult with completely developed compound eyes is able to perceive images.

Very little is known of the manner of colonization of these apterous adults or of that of the "intermediate" reproductive forms sometimes found in colonies in a regular series from forms with long wing pads (as in the nymphs of the winged forms) through forms with wing pads decreasing in length to nearly apterous forms. Usually, however, these intergrading forms are not present in such a series in colonies.

At the time necessary for brachypterous and apterous reproductive forms to leave the parent colony, workers (or nymphs) and soldiers would be attracted to these reproductive forms by the exudate, since much of the care of reproductive forms, brood and eggs by workers is due to the

fact that they derive food in the form of exudate from body secretions. In turn, they feed the adults and young, and care for the eggs. This exchange of nourishment explaining coöperative relationships of the termite castes is termed *trophallaxis* by Wheeler.

In nature, in some colonies in the Rhinotermitidae and Termitidae, a single macropterous male may be found associated with numerous egg-laying brachypterous females, the latter forms being probably utilized only because of accident to the macropterous female. That is, occasionally there is interbreeding between the different types of reproductive forms within the species in nature. Unfortunately nothing is known of the resulting progeny. In other colonies both egg-laying brachypterous females and apterous females (rarely) have been found associated together in a small colony; it is to be regretted that no associated males have been found.

No doubt in nature where one or both parent reproductive forms are lost, young reproductive forms present in the colony as nymphs are utilized in replacement. Furthermore, the development of these nymphs in an emergency doubtless is hastened by special care and feeding by the workers.

The larger macropterous reproductive adults normally are monogamous and have greater individual egg-laying capacity; the brachypterous and apterous forms are normally polygamous, but are smaller, with lesser individual egg-laying capacity; however, since large numbers of egg-laying females of the latter types are associated with a relatively small number of males, their collective power for increase in the brood is greater than that of the macropterous forms.

The results of all of the rearing and breeding experiments that have been

carried out indicate that no winged adults are produced in *pure* colonies where either brachypterous or apterous reproductive forms were the parent adults. These experiments were of from six to twenty-five years' duration and were conducted with species in several genera in the Kalotermitidae and Rhinotermitidae. Apparently these forms *breed true to type* and produce only workers and soldiers in addition to their own type of nymphs. The sexual forms take two years to develop, and in colonies of *Reticulitermes* in the United States do not appear in the first brood. Workers mature within one year, from the egg to adult, but probably do not have as long a life as the reproductive forms. From a large-headed nymph, they pass through a series of molts and quiescent stages to the adult condition.

The soldiers also mature in one year, they are few in number in the first brood and in fact always relatively few in number. Soldiers pass through a series of molts and quiescent stages from a dissimilar, worker-like prototype to the adult soldier. The change from worker-like form to soldier occurs fairly late in the development or ontogeny of the soldier caste and after this penultimate molt the soldiers, with mandibles merely for defense, never eat wood, but are fed by workers; intestinal protozoa are present as in the worker-fed young. Soldiers do not eat wood directly because they can not chew it; they are fed wood by workers and nymphs. Just how much digestion has occurred before the soldiers obtain the wood is difficult to determine.

In addition to the symbiotic relationship between termites and their intestinal protozoa, which are present in all castes in the families Mastotermitidae, Kalotermitidae and Rhinotermitidae only while they feed on wood, there are numerous insect scavengers, and various grades of insect,

arachnid and other animal "guests" or inquilines in termite colonies. These Hemipterous, Lepidopterous, Coleopterous, Dipterous, etc., inquilines range from persecuted, through tolerated, to protected, remarkable physogastric forms. The inquilines of termites have received much study by entomologists, and Emerson has extensively studied their ecology. Peculiarly modified hymenopterous parasites have been found in colonies having inquilines present which undoubtedly are their hosts; these forms have been described by Brues, Cushman and Rohwer.

In Panama in the carton tree nests of the termite *Microcerotermes arboreus* Emerson, a very peculiar Coccinelid beetle is a cared-for guest. The larvae of this beetle (*Ortalis rubidus* Gorham) are specially modified and are in the galleries with the termites except when in the pupal cell; they make the same convulsive jerky movements as do the termites, but the adult is of the ordinary type and is not modified.

There is an interesting ecological association between the termite *Nasutitermes cornigera* Motsch. and stingless bees (*Trigona nigerrima* Cresson); in Panama these bees build their nests and honeycomb within the carton tree nests of the termites, often in the center and taking up a large part of the termite nest. Any one disturbing the termite nest is assailed by swarms of these bees which, while they do not sting, bite, and are able to penetrate under clothing, into hair, etc., and make one very uncomfortable.

Certain species of termites (in the genera *Leucotermes*, *Serritermes*, *Nasutitermes* (l.s.), *Anoplotermes*, *Microtermes* and *Mirotermes*, etc.) sometimes live in the nests of other termites. The nest affords both protection and food if they are scavengers or robbers. However, they have separate galleries or smaller supple-

mentary nests of their own and never intermingle in the same nest; if they use the same galleries there is at once a fierce battle.

Further studies of these peculiar, often oddly shaped inquilines will be useful in plotting geographical distribution and relationships; apparently they do *not* occur in termite colonies in the West Indies. The basis for this symbiosis is trophallaxis or exchange of nourishment. The physogastric inquilines receive the same type of food as do the termite reproductive forms. What is its effect? A chemical study of the composition of this special food and a physiological study of its effects might prove both interesting and instructive.

Aside from predators, chief among which are the true ants, termites have no internal insect parasites, which may be explained by their protected conditions of life, the absence of resting stages and their constant activity.

Nematodes and fungous parasites occur and may result in somewhat decreasing the spread of termites. Mites are common externally on termites.

The workers and soldiers exhibit peculiar more or less synchronous, convulsive or jerky movements of the whole body when they are alarmed at a disturbance of the colony, especially noticeable when the reproductive adults appear to be in danger; this movement may also be exhibited by some of the insect inquilines. In some termites a noise is made by the soldiers by striking their heads against wood; in others, the soldiers make a noise by clicking their mandibles. It seems probable that there is some correlation between these movements and noises, and the sense organs, which are located on the antennae, bristles and hairs and pores on the legs, etc. Termites appear to be rather sensitive to vibration; seldom are

they found infesting railroad ties over which there is heavy traffic or in the wood-work of factory buildings where heavy machinery in motion would cause vibration.

Stokes (1893) has made morphological studies of the sense organs of termites and McIndoo (1923) and Hartwell (1924) have studied not only the morphology of these organs but also conducted experiments with particular reference to the location of the olfactory sense; but little is known of sense organs of termites and their reactions to various stimuli. Body odors, as well as odors related to sex, certainly have an influence on activities in the termite colony; there is a distinct acrid nest odor. Body odor, as well as contact stimuli, aid blind worker and soldier termites to maintain a single file formation (as in *Anoplotermes*) outside of the main nest, it enables them to run a straight course to a source of food and might account for other activities sometimes grouped under the heading "spirit of the colony."

Is it not possible that termites have sense or chordotonal organs located on the antennae, bristles, or at the base of the mandible enabling them to receive and respond to vibration stimuli sent through the air, or organs located on the legs to receive such stimuli through the earth? May a system of wireless telegraphy especially adapted to these blind insects exist? Of course these convulsive movements may be merely individual reactions, but the fact that the insects are blind leads one to suspect that they are a means of communication. However, what is needed is experimentation, not speculation!

Clark of the U. S. National Museum states: "I imagine that the sound, presumably with a wave length too short for us to hear, does not go either through the air or through the earth, but instead

sets up a corresponding vibration in the air pockets between the particles of which the nest is composed.

Air pockets of just the right size would vibrate in unison with any vibration that was attuned to them. Their vibration would set others in motion and thus the sound would instantly travel throughout the entire nest, indicating at once the position of the disturbance.

Organs on the legs would pick up these vibrations much more readily than organs in any other situation.

The use of resonance chambers is probably widely spread in the animal world, though there is practically no mention of them in zoological literature. In some owls the ear region of the skull is greatly enlarged with a peculiar blind pocket outside the ear openings covered by the flap. This seems to be a resonance chamber."

VIII. THE NESTS OR COLONIES

In the lower and intermediate termites, as a rule, the nests are diffused, not well-defined, and more or less temporary; colonies in these nests are more subject to migration due to unfavorable conditions. Among the higher termites, nests are concentrated and more permanent.

In the Mastotermitidae the nests are diffused and in logs or fence posts with galleries in the earth; but no species of the Kalotermitidae (except in *Hodotermes*) burrow in the earth; their nests occur on the surface in logs and stumps and far above the earth in trees and in buildings. In the Rhinotermitidae, species also (except *Prorhinotermes*) burrow below the surface of the ground where they construct a labyrinth of subterranean galleries. In species of *Coptotermes* in Australia, more or less tall concentrated mound nests are constructed above ground, while in species of the same genus in Panama, sim-

ilar nests are below ground; these are exceptions to the general rule of diffused nests among the *Rhinotermitidae*.



FIG 6 HARD MOUND TERMITARIUM OR ANT HILL OF *Armitermes medius* BANKS, 8 FEET TALL, 7 FEET IN DIAMETER AT BASE

Note the 12 feet in diameter zone cleared about the mound. April 13, 1924, Panama. J Zetek, photo



FIG 7 CARTON NEST ON GROUND OF *Armitermes chagress* SNYDER

Barro Colorado Island, C Z, Panama February 21, 1924 J Zetek, photo

Among the *Termitidae*, there are subterranean nests, very lofty or low mound

nests (fig. 6) on and below the ground level and carton nests (fig. 7) on the earth or low or high upon the trunks of trees (fig. 8).

In the United States, there are no conspicuous mound nests or arbooreal "nigger-head" or carton nests made by termites, nests of our native species are hidden within wood or below ground and termites are seldom seen except at the time



FIG 8 'NIGGERHEAD' ARBOREAL TREE NEST OF *Nasutitermes ephratae* HOLMGREN, ABOUT 3 FEET BY 2 1/2 FEET ON TREE

Barro Colorado Island, C. Z., Panama. August 22, 1923 J Zetek, photo

of the swarm. A key to these Nearctic termites is given on pages 88-9 Bulletin 108, U. S. National Museum.

Family Kalotermitidae

Species in the family *Kalotermitidae* are wood-inhabiting, being destructive wood-borers in both coniferous and hardwood timber, and do not burrow into the earth, hence they are termed non-subterranean in habit. There is no permanent

true nest and colonies are "diffused" and not concentrated. These colonies live in the moist or dry wood of dead trees, logs,

(teak) trees, in fence posts, telephone and other poles, and the woodwork and furniture of buildings. Sometimes colonies



FIG 9 CHAMBERS AND GALLERIES OF SPECIES OF KALOTERMITIDAE CUT ACROSS THE GRAIN OF WOOD

stumps, or in scars or dead areas in the trunk or in dead branches of living trees; or, more rarely (*Neotermes*) in the living wood of living valuable fruit and timber



FIG 10 IMPRESSED PELLETS OF FINE, DIGESTED, EXCRETED WOOD OF SPECIES IN THE FAMILY KALOTERMITIDAE, THESE PELLETS FALL FROM WOOD AND ARE AN INDICATION OF INFESTATION.

are found in driftwood along the seashore and along river banks.

The largest Nearctic species in the genus *Termopsis* are not very injurious. The burrows or galleries of Kalotermitidae in wood are longitudinal chambers connected by tunnels; these chambers and galleries are cut across and do not follow the grain of the wood (fig. 9). Pellets of partly digested, excreted wood (fig. 10) fill the

galleries and chambers and often fall from infested wood indicating the presence of the termites.

In certain genera the species are able to live in dry seasoned wood, such termites are called powder post termites and are potential house termites, they are very injurious to woodwork and furniture and may be carried abroad in furniture, and become cosmopolitan in so far as conditions of climate are suitable.

The reproductive forms are active and do not reach large size, they are able to move about freely in the colony and are not located in a definite chamber or locality, in consequence they are difficult to



FIG. 11. MAP SHOWING WHITE TERMITES IN THE FAMILY KALOTERMITIDAE ARE FOUND IN THE UNITED STATES.

find. The presence of slightly larger tunnels to permit the passage of the egg-laying queens, with their abdomens slightly distended, indicates that they are nearby. Also large numbers of eggs in certain portions of the nest or the localized presence of more soldiers than normal, often betray their proximity.

Both brachypterous and apterous reproductive forms occur in colonies of species of various genera in the family Kalotermitidae, the frequency of occurrence of a certain type varying with the genus. The brachypterous forms have definite color to the body and slight color to the reduced compound eyes but usually have vestigial,

shorter wing pads than occur on this type in the Rhinotermitidae, they are especially short in *Temopsis*, where the apterous form and forms intermediate from apterous to brachypterous are more common in colonies than is the brachypterous. The apterous reproductive forms have marked color to the body and slight color to the reduced compound eyes. While rare in *Kalotermites*, this type is common in *Temopsis*.

Species in the family Kalotermitidae can not migrate far and in winter do not burrow into the earth but merely penetrate more deeply within the wood in which the nest is located. Often such colonies in logs, stumps and trees are covered with ice and snow during winter.

Twenty termites in the family Kalotermitidae, representing four genera, occur in the United States, these species are found from Norfolk, Va., to Florida, westward through southern Georgia, Louisiana, Texas, New Mexico and Arizona to the Pacific Coast, where they range northward to Vancouver Island, B. C., (see map, fig. 11) and southward into Lower California.

Family Rhinotermitidae

Colonies of species of the family Rhinotermitidae are excavated in wood near or on the ground, these termites are also destructive wood borers penetrating the hardest of woods, but in addition, they excavate a labyrinth of underground passages in the earth usually near wood or vegetation, they are essentially subterranean in habit, except *Proshinotermes*, and must have a connection with the earth—the source of moisture so necessary to their life. There is no true permanent nest, as a rule, and colonies are more or less diffused throughout the wood of dead trees, in stumps, logs, scars in the trunks of living trees, fence posts, telephone and



FIG. 12.

(a) Timber in a building in New Orleans, La., reduced to the consistency of paper, the softer layers of wood have been eaten leaving the harder, (b) the wood has been honeycombed by a species of *Reticulitermes*, in the family Rhinotermitidae, where the grain of the wood is followed, (b) exit holes of winged adults of *Reticulitermes* from pine beam in infested building, Washington, D. C., (c) exit holes in earth like shelter tubes on wall of infested building, the heads of workers can be seen at the openings

other poles, and in the foundation and woodwork of buildings. Periodically inundated regions are unfavorable for these subterranean termites, but colonies are occasionally found in drift-wood. Colonies of the non-subterranean species of *Prorhinotermes* are found commonly in swamps. The galleries of these termites follow the grain of the wood, which they "honeycomb" by eating away the larger

lar, earth-like, shelter tubes of small diameter. Sometimes these shelter tubes are suspended from beams (fig. 13) or constructed upright from the floor. Usually they are on some surface such as a wall or tree trunk and often are extended for great heights.

The reproductive adults are not very active and have a remarkable post-adult growth to accomodate the enormous egg



FIG. 13

(a) Shelter tubes suspended from beam in ceiling by *Leucotermes convicinctatus* Snyder (Ancon, C. Z.); (b) Enlargement of tube (J. Zetek, photo).

celled, faster growing wood tissue, leaving the smaller celled denser wood untouched (fig. 12). Living trees and other vegetation are damaged by species in the family Rhinotermitidae, especially by species of *Leucotermes* and *Coptotermes*, which injure valuable fruit, forest and shade trees as well as growing crops. Metal, stone, brick or concrete and other substances which these termites can not penetrate are bridged over by means of granu-

tube development. Queens move about slowly but the males or "kings" are more active and usually are not found, since, while they consort with the queen in a semipermanent semblance of a slightly enlarged royal cell, they quickly desert the queen when the colony is disturbed.

In temperate regions, before winter comes, the whole colony (in *Reticulitermes*) leaves the wood and burrows into the earth below the frost line, where they

normally remain until spring, although they may temporarily come above ground during warm weather. Indeed colonies readily migrate; they change their location within the wood according to the season or with temporary changes in temperature or moisture and even the entire nest may be moved to a new site if conditions become unfavorable. In the prairie and desert regions, during periods of drought in summer when the soil is hard baked and deeply cracked, the entire colony lives in deep subterranean galleries.

In addition to the single pair of male and female reproductive adults developing from the winged forms, there are other types, namely brachypterous adults or forms with short wing pads and with more or less color to the body and eyes—its intensity varying with the genus,—(brachypterous adults are absent in *Protrichotermes*) and apterous forms; in *Protrichotermes* and *Rhinotermes* apterous adults have marked color to the body but no color to the eyes. If these adults are the parent reproductive forms, instead of there being merely a single pair, there are large numbers of females with a few males, and instead of all being in a single cell, they may be distributed throughout the colony in a series of broad cells. While these queens do not reach the large size attained by the macropterous adults, there are more of them in a colony. The queens may be located as in the family Kalotermitidae, and are often in the harder wood (such as in knots), in the interior, or in the more inaccessible portions of the wood.

In the United States, there are 12 species in the family Rhinotermitidae, representing 3 genera. These termites occur from Canada to Florida, throughout the central west, along the southern borders of the Great Lakes, and in the Rocky Mountains and Pacific Coast region. Species in one

genus (*Reticulitermes* Holmgren) occur in nearly all the states, and represent the most destructive termites in this country.

Family Termitidae

Nests of species in the highly specialized family Termitidae are located in similar places to those in the family Rhinotermitidae, namely, in wood and in the ground; some species are destructive wood borers, while others are essentially subterranean in habit and feed on vegetation in the form of plants; still others live in arboreal nests. Species of Termitidae when wood-boring in habit burrow through both decaying and sound wood; like the species of Rhinotermitidae, they require more moisture for life than do some of the Kalotermitidae.

Apparently as a rule, although their diet appears in nature to be of the same character as that of the Rhinotermitidae, they contain no intestinal protozoa that aid in the digestion of cellulose. Only in a few exceptions (species of *Armitermes*) do species of Termitidae appear to subsist on a more broken down cellulose in the form of more decayed wood or partially digested excreta. However, species of *Reticulitermes* sometimes have a similar diet. Living vegetation is injured by some of these higher termites, including trees, general vegetation and crops.

The macropterous (dealted) queens are usually in a chamber or "royal cell" (fig. 14) and are very large, inactive and practically imprisoned.

While numerous brachypterous reproductive adults of smaller size and with incompletely colored body and eyes occur, as well as "intermediate" reproductive adults, apparently no apterous adults exist; brachypterous adults are especially common in the genera *Armitermes*, *Nasutitermes* (l.s.) and *Microcerotermes*.

In the family Termitidae in the tropics,

colony life nests and food reach the highest specialization. In general, no intestinal protozoa are present in symbiotic or helpful relationship in species

Among the over specialized fungus growing termites, in addition to the royal chamber where the huge queen—mere egg laying machine—is kept in a protected

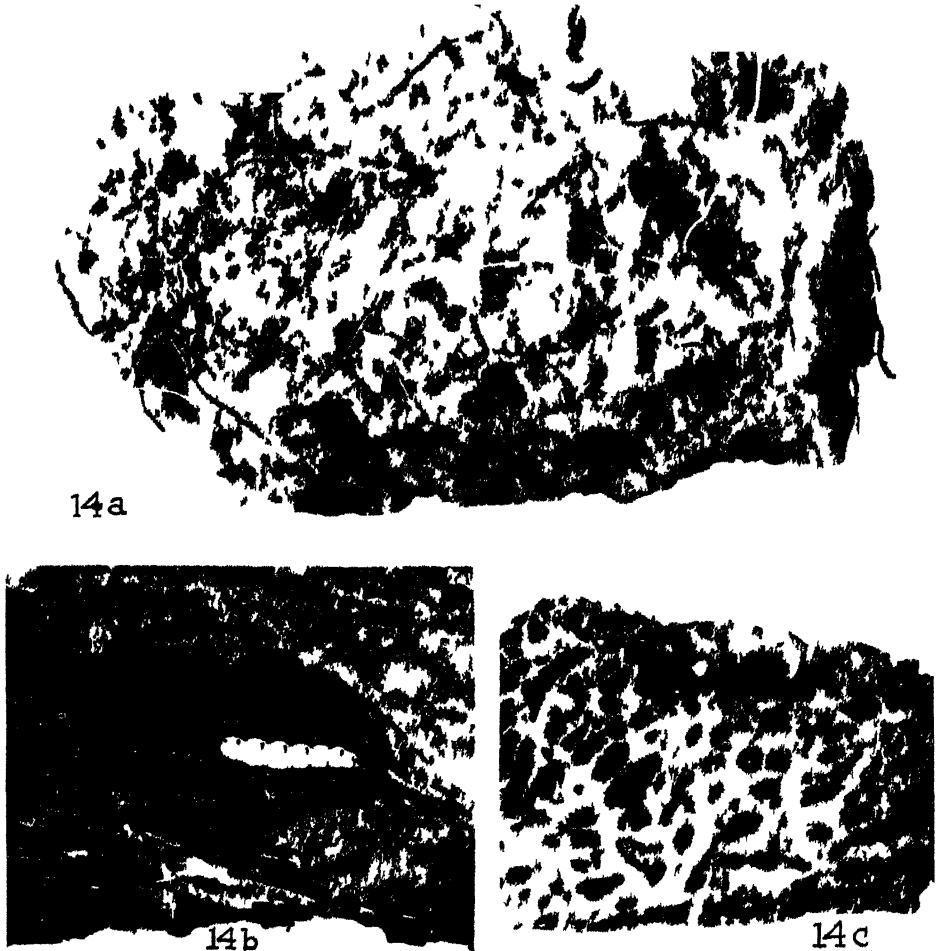


FIG 14

(a) Carton nest or termitarium of the termite (family Termitidae) *Microcerotermes exiguus* Hagen in Panama (September 7, 1923 J. Zetek photo), (b) Royal cell with dealated, macropterous queen in cell, (c) section of termitarium to show structure

of this family. Huge, hard, mound nests, and carton nests on the ground and high or low on trees (fig 14) are developed. Earth-like shelter tubes often are seen as a network on the trunks of trees (fig 15)

portion of the nest—practically imprisoned—there are special 'nurseries and fungus gardens,' where the fruiting bodies of fungi are eaten. Some of the Termitidae are foraging and harvesting in

habit and their morphological modifications show a regressive development.

Apparently the more protected and concentrated the nest and specialized the food the larger and more inactive is the queen. In the diffused nests of lower and intermediate termites the queens are small and inactive. In species of *Termit* we found the largest queens, but in the carton nests of *Nasutitermes* and *Microcosmus* the queens are relatively much larger than in diffused nests.

In the species *Microtermes panamensis* Snyder in Panama the galleries in wood are very characteristic, the wood being eaten away in a lattice-like design. Mound-like, earth-like carton nests are made on the ground or the species inhabits logs, stumps and branches on the ground or decayed places in living trees. The micropterous (decalited) reproductive forms are in a special nest like carton structure if the nest is in the wood of trees, in one large colony nine females and one male were found together, the queens averaged only 6.5 mm in length and 2.65 mm in width. Soldiers of *Microtermes* make a peculiar clicking noise with their elongate mandibles.

Microtermes panamensis is one of the few species in the family Termitidae to have possibly symbiotic protozoa in the intestines, it contains a large amoeba that ingests wood, but that apparently is not in symbiotic relation with its host.

Cleveland has proved (1923-1926) that in the lower and intermediate termites these protozoa possess enzymes for digesting cellulose, the chief food of termites. Protozoa are also found in the intestines of another Termitid (a species of *Nasutitermes*), both *Microtermes* and *Nasutitermes* are wood feeding termites and possibly obtain their protozoa through association in wood with other termites (Kalotermitidae and Rhinotermitidae) which nor-

mally contain intestinal protozoa. If such be the case, which is greatly to be doubted, the theory of a possible correlation of the phylogeny of the protozoa with that of their host termites might be weakened. According to Kirby, the amoeba in *Microtermes* could not have been obtained by associating with species of



FIG. 15 COVERED RUNWAYS ON TRUNK OF CUBAN ROYAL PALM MADE BY *Microcosmus* sp.

Ancon C. Z., Panama. J. Zetek photo. These shelter tubes extend from the ground to a carton nest on the side of the tree.

Kalotermitidae or Rhinotermitidae, since in none of the latter are any amoebae present, it came from none of the lower termites unless all these species have since lost amoebae. Despite records to the contrary, it can not be certain that there were not small amoebae and flagellates in those species of Termitidae which are recorded as free from intestinal protozoa.

For it is practically impossible to find these forms in specimens of termites preserved in alcohol. Hence, according to Kirby, it is not advisable to state arbitrarily that intestinal protozoa are absent in the highest termites—the Termitidae.

The problem of possible transfer of protozoa between species of termites is extremely important. However, the habits of termites do not suggest this possibility in nature, except where different species of termites inhabit different portions of the same nest, which is a com-

paratively rare occurrence (see page 540) under "Biology of the Termite Castes."

In the United States 10 species of Termitidae occur, representing 4 genera or subgenera. They live in wood and in the earth and do not construct mound or carton nests. Like the species of the Rhinotermitidae, they require considerable moisture for favorable conditions of life. Species of *Tenuirostritermes* in the southwestern states damage living vegetation by nocturnal foraging expeditions conducted by the workers and nasuti.

LIST OF LITERATURE

This bibliography, because of lack of space, is brief and incomplete. In general, only recent pertinent papers are included. However, in the articles listed will be found bibliographies which cover fairly well the entire field.

References to many very important articles on termites by Assmuth, Banks, Beaumont, Bequaert, Bugnion, Cockerell, Desneux, Dudley, Escherich, Froggatt, Hagen, Handlirsch, Haviland, Holmgren, Hozawa, Kemner, Knowler, Lescpès, Light, Mann, Mjöberg, Müller, Oshima, Von Rosen, Savage, Scudder, Silvestri, Sjöstedt, Smeathman, Tragardh, Warren, Wasmann, Wheeler and others, have been omitted.

The literature on termites and termitophiles is very extensive, but Emerson of the University of Pittsburgh and the writer have rather complete manuscript bibliographies which may be examined by anyone interested in the subject.

BANKS, N., and SNYDER, T. E. 1920. Revision of Nearctic Termites. Bull. 108, U. S. Natl. Museum.

BEQUAERT, J. 1925. *Neoterмес* injurious to living guava tree, with notes on other Amazonian termites. Ent. News, Vol. 36, no. 10. (Spirochaetes, two types in intestine of *Neoterмес*.)

BUGNION, E. 1913. Liste des termites indo-malais, etc. Bull. Soc. vaud. Sc. nat. (5), Vol. 49, pp. 165-172.

CLEVELAND, L. R. 1923. Correlation between the food and morphology of termites and the presence of intestinal protozoa. Amer. Jr. Hygiene, Vol. 3, pp. 444-461.

CLEVELAND, L. R. 1923. Symbiosis between termites and their intestinal protozoa. Proc. Natl. Acad. Scis., Vol. 9, pp. 424-6.

CLEVELAND, L. R. 1924. The physiological and symbiotic relationships between the intestinal protozoa of termites and their host with special reference to *Reticulitermes flavipes* Kollar. Biol. Bull., Vol. 46, pp. 177-225.

CLEVELAND, L. R. 1925. The method by which *Trichonympha campanula*, a protozoan in the intestines of termites, ingests solid particles of wood for food. Biol. Bull., Vol. 48, pp. 282-288.

CLEVELAND, L. R. 1925. The ability of termites to live perhaps indefinitely on a diet of pure cellulose. Biol. Bull. Vol. 48, No. 4, pp. 289-293.

CLEVELAND, L. R. 1925. The feeding habits of termite castes and its relation to their intestinal flagellates. Biol. Bull., Vol. 48, pp. 295-308.

CLEVELAND, L. R. 1925. The effects of oxygenation and starvation on the symbiosis between the termite *Termopsis* and its intestinal flagellates. Biol. Bull., Vol. 48, pp. 309-326.

CLEVELAND, L. R. 1925. Toxicity of oxygen for protozoa in vivo and in vitro; animals defaunated without injury. Biol. Bull., Vol. 48, pp. 455-468.

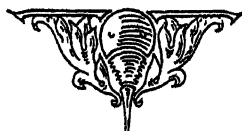
CLEVELAND, L. R. 1925. The social genius of termites. The Forum, pp. 32-40.

CLEVELAND, L. R. 1926. Symbiosis among animals with special reference to termites and their intestinal flagellates. The Quart. Review of Biology, Vol. 1, No. 1, pp. 51-60.

CRAMPTON, G. C. 1926. The lines of descent of the lower Pterygotan insects, with notes on the relationships of the other forms. Ent. News, Vol. 27, pp. 244-58. (Discusses phylogeny of termites and related groups.)

- CRAMPTON, G. C. 1919. Notes on the phylogeny of the Orthoptera. Ent. News, Vol. 30, pp. 42-8, 64-72. (Refers to Isoptera and Zoraptera.)
- CRAMPTON, G. C. 1919. Remarks on the ancestry of insects and their allies. Ontario Dept. of Agric. 50th Ann. Rept. Ent. Soc. of Ontario, 1919. Toronto. (Termites.)
- CRAMPTON, G. C. 1920. Some anatomical details of the remarkable winged Zorapterans, *Zorotypus hubbardi* Caudell, with notes on its relationships. Proc. Ent. Soc. Washington, May, Vol. 22, p. 98. (Affinities with other orders including Isoptera discussed.)
- CRAMPTON, G. C. 1920. The terminal abdominal structures of the primitive Australian termite *Mastotermes darwiniensis* Froggatt. Trans. Ent. Soc. London, pp. 137-145.
- CRAMPTON, G. C. 1920. Notes on the lines of descent of lower winged insects. Psyche, Vol. 27, p. 116.
- CRAMPTON, G. C. 1921. A phylogenetic study of the venation of the fore-wings of the Homoptera, Thysanoptera, Psocida, Zoraptera, Neuroptera, Embiida, Plecoptera and Hadenomoida—with notes on the Hymenoptera and Coleoptera. Ent. News, Vol. 32, pp. 97-105. (Isoptera, p. 99.)
- CRAMPTON, G. C. 1921. A further comparison of the wings of Zoraptera, Psocids and Aphids from the standpoint of phylogeny. The Canadian Entomologist, Vol. 53, pp. 110-117. (Phylogeny of termites discussed briefly.)
- DESNEUX, J. 1904. À propos de la phylogénie des Termitides. Ann. Soc. entom. Belg. T. 48, pp. 278-286.
- EMERSON, A. E. 1925. The termites of Kartabo, Bartica District, British Guiana. Zoologica, Vol. 6, pp. 291-459.
- ESCHERICH, K. 1909. Die Termiten oder weissen Ameisen. Leipzig, Werner Klinkhardt, 8°, 198 pp.
- FEYTAUD, J. 1920. Sur les jeunes Colonies du Termite lucifuge. C. R. Acad. Sci. Paris 171, pp. 203-6.
- FEYTAUD, J. 1924. Le Termite de Saintonge. C. R. Acad. des Scis. Seance 7, pp. 241-4.
- FEYTAUD, J. 1925. Existe-t-il Plusieurs Races de *Reticulitermes lucifugus* Rossi? Revue de Zoologie Agricole 24 Année, no. 8, pp. 161-9.
- FULLER, C. 1915. Observations on some South African termites. Ann. Natal Mus., Vol. 3, pp. 329-504.
- FULLER, C. 1919. The wing venation and respiratory system of certain South African termites. Ann. Natal Mus., Vol. 4, p. 19.
- FULLER, C. 1920. Studies on the post embryonic development of the antennae of termites. Ann. Natal Mus., Vol. 6, pp. 235-295.
- FULLER, C. 1921. The termites of South Africa being a preliminary notice. So. African Jour. Natur. Hist., Vol. 3, pp. 14-52.
- FULLER, C. 1924. The thorax and abdomen of winged termites. Dept. Agric. Union of So. Africa Entomology Memoirs, Memo. No. 2, pp. 49-78.
- GRASSI, B., and SANDIAS, A. 1893. Costituzione e Sviluppo della società dei termitidi, etc. Dagli Atti dell Acad. Gioenia di sci. nat. in Catania, Vol. VIe ser. 4° Catania.
- HEATH, HAROLD. 1902. The habits of California Termites. Biol. Bull., Vol. 4, pp. 44-63.
- HUGH, E. 1922. Les Termites. Sept., Bruxelles. (A complete, illustrated compilation of data on termites, with bibliography.)
- HILL, G. F. 1921. New and rare Australian termites with notes on their biology. Proc. Linn. Soc. New South Wales, Vol. 46.
- HILL, G. F. 1925. Notes on *Mastotermes darwiniensis* Froggatt (Isoptera). Proc. Roy. Soc. Victoria, Vol. 37 (N.S.), pp. 119-124. (Eggs laid in masses cemented together as in roaches (Blattidae).)
- HOLMGREN, N. 1909. Termitenstudien 1. Anatomische Untersuchungen. K. Svenska Vetensk. Akad. Handl., Bd. 44, p. 215, Taf. 1-3, Uppsala and Stockholm. Die Verwandtschaftsbeziehungen der Termiten, pp. 208-213.
- HOLMGREN, N. 1910. Versuch einer Monographie der amerikanischen Eutermes-Arten. Mitteil. aus dem Naturhist. Mus. Hamburg, Bd. 27, pp. 171-325.
- HOLMGREN, N. 1911. Termitenstudien 2. Systematik der Termiten. K. Svenska Vetensk. Akad. Handl., Bd. 46, pp. 86, Taf. 1-6, Uppsala and Stockholm. Ordnung Isoptera, p. 10-11.
- HOLMGREN, N. 1912. Termitenstudien 3. Systematik der Termiten. Die Familie Metatermitidae. K. Svenska Vetensk. Akad. Handl., Bd. 48, 166 pp., Taf. 1-4, Uppsala and Stockholm. Blick auf dem mutmasslichen, stammesgeschichtlichen Entwicklungsverlauf der Termiten, p. 129-353.
- IMMS, A. D. 1919. On the structure and biology of *Archotermopsis*, together with descriptions of new species of intestinal protozoa and general observations on the Isoptera. Philos. Trans. Roy. Soc. of London, ser. B, Vol. 209, p. 75. (*Archotermopsis wroughtoni* Desn. in British Garwhal in the Himalayas.)
- JUCCI, C. 1920. Sulla differenziazione della caste

- nella societa dei termitidi i neotenici. Atti R. Ac. Naz. Lincei, Anno 317, pp. 95-8.
- JUCCI, C. 1924. Su la differenziazione de le caste nella Societa dei termitidi. Reale Accad. Nazionale dei Lincei (Anno 320, 1923), Serie quinta, Vol. XIV, Fasc. IX, Roma.
- JUCCI, C. 1925. Il problema dei reali veri del *Reticulitermes lucifugus*. Bollet. della Soc. Entomolog. Italiana Anno 57, pp. 98-107. (Bibliography.)
- KNOWER, H. Mc. E. 1894. Origin of the "Nasutus" of *Entermes*. Johns Hopkins Univers. Circ. 13, pp. 58-59.
- SNYDER, T. E. 1919. Some significant structural modifications in nearctic termites. Proc. Ent. Soc. Wash., Vol. 21, pp. 97-104.
- SNYDER, T. E. 1920. The colonizing reproductive adults of termites. Proc. Ent. Soc. Wash., Vol. 22.
- SNYDER, T. E. 1924. "Adaptations" to social life: The termites (Isoptera). Smithsonian Miscellaneous Collection, Vol. 76.
- SNYDER, T. E. 1925. The origin of the castes in termites. Proc. Biol. Soc. Wash., Vol. 38, pp. 57-68.
- SNYDER, T. E. 1925. Communism among insects. Scientific Monthly, Vol. 21, pp. 166-177.
- SNYDER, T. E. 1925. Notes on fossil termites with particular reference to Florissant, Colo. Proc. Biol. Soc. Wash., Vol. 38, pp. 149-166.
- SNYDER, T. E. 1926. Races or sub-species in *Reticulitermes*. Proc. Biol. Soc. Wash., Vol. 39, pp. 1-6.
- THOMPSON, C. B. 1917. Origin of the castes of the common termite, *Leucotermitis flavipes* Kol. Journ. Morph., vol. 30, pp. 83-136.
- THOMPSON, C. B. 1919. The development of the castes of nine genera and thirteen species of termites. Biol. Bull., Vol. 36, pp. 379-398.
- THOMPSON, C. B., and SNYDER, T. E. 1919. The question of the phylogenetic origin of the termite castes. Biol. Bull., Vol. 36, pp. 115-132.
- THOMPSON, C. B., and SNYDER, T. E. 1920. The "third form," the wingless reproductive type of termites: *Reticulitermes* and *Proterhinotermitis*. Journ. Morphology, Vol. 34, pp. 591-633.
- THOMPSON, C. B. 1922. The castes of *Termopsis*. Journ. of Morphology, Vol. 36, pp. 495-531.
- WHEELER, W. M. 1918. A study of some ant larvae, with a consideration of the origin and meaning of the social habit among insects. Proc. Amer. Philos. Soc., Vol. 57, pp. 293-343.
- WHEELER, W. M. 1923. Social Life Among the Insects. New York





AGE AND AREA

By J. C. WILLIS, F.R.S.

[THE QUARTERLY REVIEW OF BIOLOGY has no intention of boring its readers with polemics. But the attack on the Age and Area hypothesis in an earlier number presented such an extremely one-sided view of the matter that it seemed desirable to restore the balance. Accordingly we have asked the distinguished originator of the theory of Age and Area, Dr. J. C. Willis, to prepare the following article. We now intend to give our readers ample time fully to digest and assimilate this two-course meal before offering them any more *pabulum* flavored with Age and Area.—THE EDITOR.]

ABOUT four years ago, under the above title (from the principal thesis therein brought forward) I published a book which has aroused some controversy and much criticism. Whether my views be accepted or not, they have reawakened interest in the fascinating study of geographical distribution, which for a long time has been in undue abeyance, and much new and valuable work has been brought out.

My principal thesis, "Age and Area," is based upon *statistics*, whose introduction into biological work is sometimes resented, though one is becoming used to their employment in Mendelism, in agricultural research, etc. Many years ago, Hooker published a statement to the effect (14, vol. i, p. 438) that "All seem to resent the making botanical geography too exact a science; they find it far easier to speculate than to employ the inductive process. The first step to tracing the progress of the creation of vegetation is to know the proportions in which the groups appear in different localities, a relation which must be expressed in numbers to be at all tangible." My work has consisted largely in following up this suggestion, and in showing in what manner the careful use of statistical methods can be applied to aid

the various ways—morphological, ecological, and other—already in use for the investigation of the complex problems of botanical geography.

My statistics, which might otherwise have been dismissed as those of an amateur, have received great support from the fact that they have been taken up by the well known statistician Mr. Udny Yule, who has based upon them an important paper (33).

As I have pointed out in the first sentence of my book, "The existing distribution of a plant (or animal) upon the surface of the globe, which is often a very complex phenomenon, is due to the interaction of very many factors;" and at the end of the same paragraph I have said, "To all this it is obvious that age must be added—the older a species is, the more area will it have had time to cover." People have often taken up Age and Area *alone*, as if it, without assistance from other branches of knowledge, were expected to provide a master-key that had only to be turned in the lock to open a main avenue to the solution of the problems of geographical distribution. These problems are among the most complex and puzzling of all that arise in biology, and without the application of all the various criteria that are available—morphological, cytological, ecological,

and all the rest must also be applied—Age and Area will only lead to disappointment. Too much is expected of it, and because it alone will not explain the distribution of a family like the Magnoliaceae, that has passed through many geological periods, and many climatic and other vicissitudes, or explain the limited areas of such local endemic species as those of the Gulf of St. Lawrence, or the scattered woody endemics of parts of the United States, it is rejected as valueless. I have not laid stress in my papers on the employment of these other criteria because I have taken it for granted.

DEVELOPMENT OF AGE AND AREA

It may be well, as a preliminary, to consider briefly how "Age and Area" was arrived at, and matured, after some twelve years of work upon the flora of Ceylon. I very soon noticed that the local endemic species, which make up some 27 per cent of the flora, were rare—a very remarkable fact when they were (at that time) supposed to be specially adapted to the local conditions. Trimen, the author of the Ceylon flora, divided them into six classes, VC, C, RC, RR, R, and VR (very common, common, rather common, rather rare, rare, and very rare), largely by the extent of their distribution in the island, except that VC and C covered the same areas, the former being commoner upon the ground. If one unite these two, one gets five classes. To verify my final statistical results, obtained by adding up the whole flora, I took the flora of New Zealand (Cheeseman), using actual longitudinal measurement of range in these long narrow islands, and made ten classes. Adding these together two by two, one obtains five, to compare with the Ceylon figures. Dividing the Ceylon flora into (1) endemic, (2) occurring in Ceylon and South India, and (3) going beyond this,

and the New Zealand flora into (1) endemic, (2) wides reaching New Zealand only, (3) endemics reaching the islands round New Zealand, and (4) wides doing the same, one gets the following table:

NEW ZEALAND					
CLASSES	1	2	3	4	5
1	104	168	683	112	70
2	128	114	313	120	9
3	133	87	209	184	7
4	190	66	159	190	4
5	232	79	144	296	4
Average	rarity . . . 3.4 2.7 3.4 2.3 1.5				

The wides are most numerous at the top, the endemics at the bottom, and the columns are *graduated* from one end to the other. In other words, the wides are the most widely distributed in Ceylon, the species occurring in South India next, and the endemics least. In New Zealand the wides that reach the outlying islands are most widely distributed, the endemics that do the same are next, and then follow the wides that do not, and the endemics that do not.

Now such figures as these are very striking, and they require explanation, especially as similarly graduated figures turn up in a number of other cases. There must be some reason for their graduations, and for the great differences shown by the various classes of plants, endemic or other. Statistics, as these are, are quantitative data, affected by many factors, but when they show a definite graduation like this, there is most probably to be seen the effect of one factor—alone, or principally. Now it is all but impossible to suppose that these figures show the effects of adaptation, or of natural selection—these would

hardly be nicely graduated. It is open to anyone to propose any explanation of them, but so far the only other explanation than mine is that they are due to pure chance. This however does not explain why wides and endemics differ. My explanation is that *on the average of numbers of allied forms* (for the figures show in the same graduated and differential way for single families or for large genera) the effect may be broadly put down to age. Age in itself effects nothing, but it represents the resultant effect of all the various forces that are acting upon the distribution—dispersal methods, adaptation to climatic and biological factors, progress of the association to which the plants concerned happen to belong, and so on. If one suppose that the wides of Ceylon are the most widely distributed there because *on the whole* they arrived first in the island, the South Indian species next because they arrived *on the whole* later than the "wides," and the endemics least because they were *on the whole* evolved later still, one obtains a conclusion which fairly well explains all the facts that are to be seen in the statistical tables. But these are general results, only valid for groups of allied species, and quite inapplicable to individuals. Many endemics will have been evolved in Ceylon before all the wides have even arrived there, and will have reached the maximum degree of commonness. Other endemics will have been evolved upon isolated mountain tops, and even though very old will not have spread beyond their first location. But on large numbers the facts come out clearly enough.

Finding that similar statistical results appeared in many different floras, I drew the general conclusion that Age and Area was applicable, not only to one country, but to the world; but one must always deal with matters in a statistical way, and not try to apply conclusions to small

numbers. Similarly, finding that in the statistics, size of a genus went with the area occupied, when one took them in groups of allies, I formulated the rule which I have called Size and Space.

GENERAL ANSWER TO CRITICISM

I. Constant conditions

A great deal of adverse criticism has appeared, and it is not altogether easy to understand why Age and Area has met with so much reprobation. That if more time be allowed for the active factors in distribution to carry on their work, more area will be occupied, seems a very harmless and all but self-evident proposition, and it was clearly put forward by Grisebach, followed by Lyell and Hooker. As I have pointed out (AA, p. 6) "the *resultant* effect of all the active factors, like dispersal methods, etc., is so uniform, when one considers long periods of time, and takes an average of several allied species, that these species spread indefinitely at a fairly steady average rate. This rate . . . will probably not be the same for any two species, but for allied forms will not usually differ very much, so that by taking groups of ten allies, and comparing with other groups allied to the first, the rate of expansion of area will be a fair measure of age."

The general answer that may be made to criticism is that the hypothesis is based upon statistics, and must be handled *quantitatively*, and that the provisos with which I have hedged it about must not be ignored. Yule defines statistics as "quantitative data affected to a marked extent by a multiplicity of causes." Only by taking numbers can one hope to perceive any result that one may interpret as due to one of these causes, and one must always deal with numbers if one hope to get results of any value. For some inscrut-

able reason, the fact that I have made provisos at all seems to arouse hostile criticism. Had there not been these provisos it would have been so easy to upset the hypothesis, and though my critics often begin by mentioning the provisos, they usually end by ignoring one or more of them, and sometimes all, completely.

On page 63 of my book, the hypothesis is thus stated: "The area occupied (determined by the most outlying stations) at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man, and by other causes."

Now most of my critics are inclined to lose sight of these provisos, upon which I have always insisted. If they be neglected, it is easy to find facts that are quite incompatible with Age and Area, and special attention must once more be called to them. The first is "so long as conditions remain reasonably constant." It is of course all but impossible for them to remain exactly constant, but they may be much the same on averages of say ten years, and so long as that average does not show a steady and marked change in one direction, I should class the conditions as reasonably constant, though the rainfall, the sunshine, the ecological conditions, etc., may vary from month to month or from day to day. Such conditions occur, for example, in the great tropical forests, in the moorlands of Europe, in the deserts of the southwest United States or in the Yellowstone Park, places where man is not continually interfering with his agricultural, warlike, and other activities,

and where the secular change of climate is extremely slow.

It must of course be remembered that the chief obstacle to rapid distribution is probably the presence of definite associations of plants over large areas, but even here, as Clements says, "the most stable association is never in complete equilibrium." Here the changes of conditions are going on more or less in a definite direction, but so slowly that I think one may regard the conditions as reasonably constant.

Careful adhesion to this first proviso renders nugatory many of the criticisms that have been made, for my critics have taken the case of plants that have gone through many vicissitudes of climatic and other change, like the plants of the Gaspé region, which have at any rate been more or less surrounded by ice on one or more occasions, or the family Magnoliaceae, which have survived many changes. In such cases, Age and Area *alone* can give no result that is worth consideration, unless one can trace by aid of the fossils the area that has been covered, and that sometimes twice or more. If plants have been compelled to migrate back and forward by alternations of ice and of warmer periods, the area really covered may be represented by *several superposed folds*, a fact that is usually completely lost sight of. In regions seriously affected by glacial periods, Age and Area may be regarded as inapplicable until we can trace all the migrations, but the nearer to the Equator one goes, the more useful does it become. In the north there are many endemics of very isolated forms, that may be regarded as real relics, but in the equatorial regions these are but few and there are vast numbers of endemic species that are closely related to their surrounding species, whether endemic or wide. These forms enormously outnumber the relics of more

northern countries. H. A. Gleason (7, bottom of p. 544) says that "it is essential to the validity of Age and Area that migrations be always forward." This I fail to grasp, but as I have just pointed out, much must not be expected of Age and Area in regions where migration, usually due to ice action, is common. With the go and come of the ice, a species might easily have migrated three or four times over the same ground, and unless one could trace its progress accurately with the aid of fossils at different levels, one might go very far astray. If the ice advance rapidly, as is often supposed to have been the case, some species will not be able to migrate fast enough to escape extermination, while others will already be so far ahead of the ice, or so rapid in movement, that they will survive. In the Old World there is a vast mountain barrier from east to west, against which many species might be killed out altogether, while in America there is room for migration much further to the south.

Further than this, the oncoming and subsequent retreat of the ice seems often to have made a definite change in the climate and other conditions, rendering life less favorable to the growth of the (generally) woody or arboreal forms that previously occupied the ground, and which, like so many of the local woody endemics in the flora of the United States (*cf.* AA, footnote, p. 86) now survive in the midst of conditions that are generally unfavorable. Since the ice retreated, man has occupied the ground, further increasing the unfavorable conditions.

But it is not only a change of climate that has affected these plants. The invasion of the ice has usually broken up or destroyed the old associations in which they used to live, and in consequence of this, their rate of distribution must probably have become enormously slower than

under the old conditions. In fact, it is not improbable that the changed conditions offer a complete barrier to further distribution. In any case, one will not expect to see any serious extension of area unless the old association can be largely reconstructed, or unless the species can force its way into some new association, for which the pioneer species will prepare the way. These endemics, which after all are few compared to the multitudes of non-relic endemics, are local, like the most of the Ceylon endemics, simply because there has not yet been time for them to be anything else, even when they are not checked by the barriers of climatic and other change. But their previous history may be written in the fossils, and must be followed there.

The old idea (encouraged by the rapid spread of weeds in cultivated ground, where the original plant associations have been completely broken up) that distribution is very rapid, still holds a large sway, but as I have endeavoured to show (AA. pp 19-22, and Chap. V) there is little or no justification for the taking up of this attitude towards the subject. Distribution in general, over ground more or less fully occupied by associations of plants, will be an extremely slow process, and it does not in the least surprise me that so many plants in various regions of the United States, which must of course be regarded as relics left by the ice age, should still be confined to the places (perhaps a little extended) in which they were left. They are in general surrounded by associations that are probably different from those in which they lived, and one will expect them to spread, if at all, with the most extreme slowness. The present tropical forests go back probably before the ice age, yet they contain many endemics that have only spread a very short distance, though the conditions have been favorable.

One of the things that I am fighting for in my advocacy of Age and Area is to get the idea accepted that distribution is a dynamic process, which is still going on. It is not, in my opinion, a phenomenon that takes place so rapidly that most things have already reached their limits of possible distribution. They have reached so far as age (representing the resultant of all the active forces in distribution) can carry them up to the present time, against the influence of the various barriers—physical, ecological, and the like—that check or oppose their distribution.

This same proviso as to constant conditions of course really disposes of any attempt to consider by aid of Age and Area alone such cases as those of *Sequoia* and many other plants which have gone through two or more geological periods, for they can hardly have escaped being affected by great changes of conditions during so long a time, and we cannot always say from the fossils exactly what their migrations may have been. Here again, to look upon distribution in a dynamic way will somewhat change our views upon the subject. As I have pointed out (AA, p. 88), there is hardly a more suitable conifer for general sub-tropical conditions than *Cupressus macrocarpa*, which has been planted in millions over the mountains of the tropics, and in other places of like conditions. And yet, if one examine it in its only *native* habitat, one is forced to conclude that it is, *there*, a species that is dying out, on account of unfavorable conditions. Had it not been taken up by man for planting in conditions that are more suitable to its growth, there can be little doubt that it would ultimately have disappeared, and would have been counted from the fossils as one of those species to which the world was no longer suitable. It is not to the world,

but to the conditions that have supervened in the regions where they were growing, that species like this, or *Sequoia*, have become unsuited; they have not been able to spread quickly enough to reach more favorable localities, or these may have been too far away to have been reached in any case. As the world grows older, the climate tends to become drier, and shows more differentiation, and this alone has localized many forms that in more uniform climates would have occupied much greater areas. At the same time, differentiation of species seems to accompany differentiation of climates, and as Hurst has shown with regard to *Rosa* (16), the original species, carrying the possibilities of resistance to different types of climate, seems gradually to differentiate into species suited to one only.

A careful taking into consideration of my first proviso is thus a sufficient answer to many criticisms. How closely, even in the far north, recent species, evolved since the conditions became pretty much what they are now, may follow the rule, may be seen from the work of Samuelsson (22), who shows the way in which endemic plants—in this case *Hieracia*, and evidently of recent formation—spread from centers where they are (at present) comparatively numerous, and occupy scattered locations round about. His map of the distribution of one of these microspecies, here reproduced, shows this very well, giving the actual spots in which it has been found in a country well worked for *Hieracia*. The further one goes from the center of distribution, the more scattered become the locations, and Samuelsson also remarks (reprint, p. 6). "In den Standorten an den Grenzen des Verbreitungsbezirkes scheint die Anzahl der Individuen kleiner als im Centrum zu sein. Mindestens ist dies der Fall in Dalekarlien, wo zwei Standorte bekannt sind." This is what

one would expect, on the general principles which I have endeavored to make clear in Chapters II to V of my book. The more closed the associations of plants become, the slower will be the dispersal, but every now and then a species will get a foothold in a new place, often, it may be, at a considerable distance from any other members of the same species. In the map just given, the most isolated locality is separated by about 20 miles from the next, though of course one cannot be certain that there is not, and never has been, an intermediate position.



DIAGRAM A. Distribution of *Hieracium chloroleucum* Dahlst.

On page 10 Samuelsson goes on to explain this remarkable distribution, and says "ist meiner Ansicht nach das geringe Alter jener Sippen die wichtigste." Here then is another anticipation of my detailed publication of *Age and Area*, though my own first suggestion of it was in 1907, and as I have pointed out in my book (p. 3), Lyell and Hooker published the general idea in 1853, whilst Samuelsson points out that Grisebach (9), six years earlier, calls attention to plants that are so young that they have not yet had time

to be distributed far from their point of origin.

Samuelsson points out that the conditions in much of southern Sweden are practically the same as those where these very local species at present exist, and that there is no reason to suppose that they would not succeed over much larger areas than those which they actually occupy. He also points out how often single plants or clumps of individuals of new and distinct forms have been found, and have never been found again, in spite of much searching. He takes the same view of this as I have taken in my book upon page 151, that the collection of the specimens exterminated the species, a view which Dr. Guppy has also proposed to me to account for the many species only once seen, and never found again.

Samuelsson then goes on to point out that the distribution of these *Hieracia* negatives the idea that it can be in response to an adaptation to local conditions (cf. AA., pp. 231, 148, 87, etc.). and that though they are obviously very young, no intermediate forms can be traced, even in the case of such a very local form as *H. microcymon*, which he regards as evolved since the arrival of man in Sweden. He regards the forms as having arisen by mutations, and says "Das Alter der Sippen der *acroleucum*-gruppe scheint der Grösse der Verbreitungsbezirke ungefähr proportional zu sein. Es ist deswegen wahrscheinlich, dass *H. acroleucum* die älteste Sippe dieser Gruppe ist. Vielleicht sind alle übrigen Sippen der Gruppe aus *H. acroleucum* entstanden." This is the point of view that I have taken for many years (cf. 26-29) and which I am once more bringing up in recent papers (30). The original idea goes back at least to G. St. Hilaire, and, as is well known, species were always supposed to arise suddenly in the days of special creation.

The gradual development of them is an assumption brought up by Darwin and his supporters in this matter; and is as yet without proof.

Samuelsson also suggests that some of the very isolated localities may be due to another appearance of the same mutation, a possibility that appears not improbable when one has realized for example the way in which the mutant *gigas* appears again and again in de Vries' cultures, or considers how likely it is that the same change in the nuclear constitution may happen twice, especially perhaps in nearly related forms such as these *Hieracia*.

Samuelsson's whole paper is very interesting, and deserves to be more widely known. He ends by pointing out, with a map drawn from Wettstein's own localities for gentians (23), that the latter's widely accepted opinion, that species arise as adaptations to local conditions, and do not overlap, is not sound, for there is in fact considerable overlap. The maps agree much better with the view of origin by mutation, and gradual dispersal from the centers of origin. Arguments based on Wettstein's published opinions require careful examination with the facts.

II. Consideration of groups of allied species

The next proviso in my statement of Age and Area is as important as the one which has just been considered, and though from the very beginning I have strongly insisted upon it, it is very often ignored by my critics. It is that one must always deal with "*a group of allied species at least ten in number.*" This again disarms much of the criticism that has been directed against Age and Area. Practically all the local woody endemics mentioned above for the United States, for example, or those of the Gulf of St. Lawrence, are rendered valueless for purposes of argument, inasmuch as they can-

not be placed with the needful number of allied forms to make up a group of ten close allies—in many cases they cannot even be placed with others of the same family—nor are there other ten, nearly allied to them, with which to make a comparison. This point, too, I have especially insisted upon (*cf.* AA. pp. 85-6). If a group of ten allied *Dipterocarpus* trees, for instance, cover an area (sum of all ten areas) of 100,000 square miles, and another group of ten allied to the first, and in the same country, cover 200,000 square miles, then Age and Area indicates that the second group, as a whole, will be older there than the first, and if the alliance be very close, and the conditions very similar, will quite probably be more or less twice as old. But *one cannot compare individual cases.*

The whole theory is one of statistics, and statistics, by their very nature (for they are *quantitative* data) are not applicable to individual cases, but only to groups. It is only when one takes the data quantitatively that one can perceive that age shows an effect which may be numerically represented. With statistics one sees the effect of age, without them one can only speculate upon it. In the case of a solitary individual species, so many factors are operative, that the effect of no single one can be picked out with certainty, though all kinds of speculative or theoretical views may be put forward as to the causes that have operated to produce this or that effect. But when one takes large numbers, and finds the totals varying in a direction that seems only explicable as the effect of age, then one becomes justified in proposing age as an important factor in distribution, and in pointing out certain results as being probably due to it. The results that show very clearly with large numbers also show so well with smaller numbers, when one takes close allies and

compares them with other allies, closely allied to the first, that one is also fairly justified in fixing a number like ten as a minimum. But these ten *must* be closely allied, and *must* only be compared with other groups of ten allied to the first. The exclusion of individual cases from consideration throws out at once a great

or even for a group of two or three, is wholly to misunderstand the principles underlying statistics and their use.

Let us take the very simplest case that it is possibly to imagine. Suppose that ten species of a genus *A* all commence in the same country at the same moment *X*, and another ten of a genus *B*, as closely

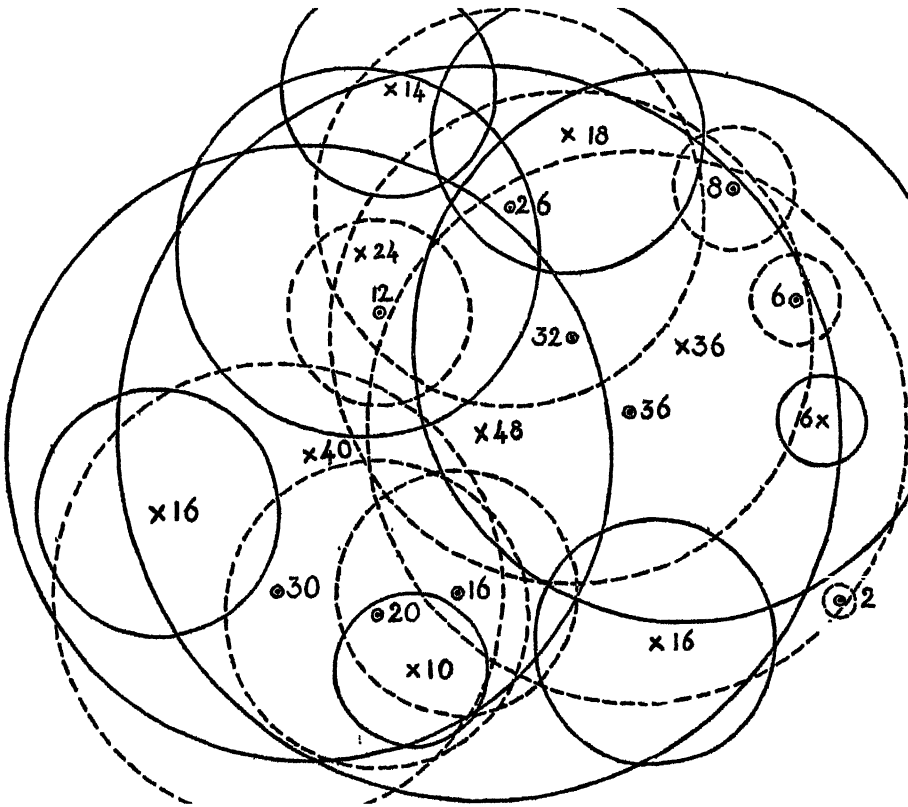


DIAGRAM B. (For explanation see text)

proportion of the objections that have been brought forward.

Individual species differ so much in their reactions to the surrounding conditions that probably no two are distributed at the same rate, except at times accidentally, and to reason from the hypothesis of Age and Area for an individual species,

allied to *A*, and as much like it in every way, as possible, all start at the same moment *Y*. The problem before us is to determine which moment, *X* or *Y*, was the earlier, assuming the correctness of Age and Area. Let us further suppose that each species has spread uniformly round its point of origin, so that we

can work with the diameters of the circles thus formed. Then we begin by measuring the diameters of the various circles, which look a hopeless intermixture. Arranging them in order of size, we get the result

A (cross at centre, solid line):

48 40 36 24 18 16 16 14 10 6

B (dot at centre, dotted line):

36 32 30 26 20 16 12 8 6 2

The ten species of *A*, though starting at the same time, differ so much in capacity of dispersal, in luck in meeting suitable conditions, and in other ways, that the areas they occupy vary between 6 and 48 in diameter (I imagine that so great a difference possibly would not often occur between species starting at the same time in the same country, but it makes the argument clearer), while the *B* species vary between 2 and 36, and three of them at least show areas much greater than those of two thirds of the *As*. Yet when one totals the whole numbers, one finds that the *As* add to 228, the *Bs* only to 188. And it is on this result that Age and Area says that the *As* as a whole are probably older than the *Bs*. But it is obvious that one *cannot* draw any conclusion about the individual areas.

Still more obvious is this, when one remembers that the ten *As* may with practical certainty be assumed to have commenced in the country at different times, and the ten *Bs* likewise. On the whole the ten *As* will be older than the ten *Bs*, but beyond that Age and Area cannot go with any probability of safety. It is obviously impossible to reason—one can only guess—about the individual species that make up the tens.

This explanation will, I hope, help to make clear the general statistical principle upon which Age and Area is based. The explanation upon page 62 of my book should also be read in this connec-

tion. In my earliest papers I fixed at 15–20 the number of allied species with which one ought to deal, and I am not sure it might not be safer even now to return to these figures. Or perhaps it would be more correct to say that the further one goes from the equator the larger the number that one should use. Individual species from these two lists (*A* and *B*) may be made to prove *anything* if Age and Area alone be applied to them, but this is not the case with the totals, and it is with these alone that statistics have any concern.

It is for similar reasons that when comparisons have to be made, one must only compare one group of allied species with another group closely allied to the first. If one try to compare species of different families, or belonging to different types of vegetation, the range of variation may be vastly greater than in the imaginary case that we have just been considering, and a very much greater number of species must be taken together. Even then the result will be valueless if we do not ensure that they belong to somewhat similar types of vegetation. Even employing a few hundred or more at once, I should feel sceptical of any value in the result obtained. One of my critics, for example, is doubtful of Age and Area because (quoting Ridley) I have said that a certain *Dipterocarp* tree would take 60,000 years to travel 100 miles, while the *Conifer* forest of North America travelled a much greater distance in much less time. But the two groups are in no way related, have different types of seed, and live in different countries and conditions, and *cannot* be compared. A note in *Science Suppl.*, March 3, 1926, p. x, gives figures for dispersal of seeds of the Douglas fir. Unfortunately the height is not given, but Ridley's tree was 100 feet, and while he found that even in strong wind the seeds

did not go beyond 100 yards, the fir seeds, in an eight-mile breeze, fell in maximum quantity at 360 yards, and some overpassed the observers at 530 yards. Groups of plants must be compared, and even then only the closest relatives, living in closely similar conditions.

A paper by Calvert (2) illustrates this disregard of my provisos, and shows that like others, he expects too much from Age and Area, having taken it up as if I had proposed it as a substitute for all other methods of dealing with the problems of distribution. He ignores the proviso which we have just been considering, and also seems somewhat in doubt as to the application of the figures. On page 221, for instance, he quotes figures for distribution in New Jersey, and applies them generally. On the next page he takes figures for the world, and applies them to individual genera, thus finding that *Argia* should be the oldest—a result contradicted by morphological evidence. If the whole group of allies to which *Argia* belongs is the largest and the most widely distributed, then it is probable from Age and Area that as a whole it is older than another group closely allied to it and less numerous and less widely distributed. But one cannot argue about individual cases, and one must take age, size, and area together, not in two separate compartments.

III. Barriers

We now come to the reservation about *barriers*, that the action of Age and Area may be enormously modified by their presence. This is obvious in the case of sea, for only a few species are occasionally and with difficulty able to pass across any serious width of salt water (cf. Guppy's books). "For the case of floras (plants in ecological association) Dr. Willis rightly insists that land connection, complete or

all but complete with the source of dispersal, at the time of dispersal, is necessary" (Mrs. Reid, AA, p. 139). This can hardly but be admitted by anyone who has studied the subject. An endemic, starting, as so many have done, upon an island, has only the very remotest chance of ever spreading beyond the confines of that island; though, as a matter of fact, few have even yet covered the local areas possible to them in the larger islands like Ceylon or New Zealand.

Mountains, again, in the form of chains, may afford very considerable barriers to progress, especially when, as is so often the case, the climates differ on the two sides.

Then there are the many ecological barriers. A plant will in general find it difficult to enter another association than that to which it usually belongs, and so will be largely determined in its distribution by the rate of progress of the whole association, which may often cease to move for long periods at a time. Hence again, the absolute necessity of dealing with groups of ten allies, so as to allow for differences of this kind. The whole ten will rarely be confined to one association.

But I have said enough about barriers in my book, and it will suffice to have drawn attention to the obviously enormous differences that they may make in the distribution of plants about the world. An endemic of a single mountain peak, extending some distance above the general height of the chain, may easily be barred from ever extending beyond it, if it is not suited to life at somewhat lower levels (cf. Gleason, l.c.).

In what has been said, I hope that I have made it clear that one must work with great caution and circumspection in applying the rule of Age and Area. Some who have now contemptuously rejected

the whole thing have taken it up as if it had been proposed as a master-key to the problems of distribution—as if it were to be simply a case of “measure a few areas and there you are,” leaving morphological, ecological, and other criteria out of consideration.

Some systematists hold the opinion that because what were once accepted (by such masters of systematic botany as Hooker, for example) as general species, ranging enormous areas, are now being split into smaller species of more limited range, Age and Area can no longer hold. As I have already pointed out (AA, p. 98, objection 29) such work really strengthens the position of the hypothesis. The more local the species “become,” the more clearly do they show the effects of age in their dispersal (cf. the work of Samuelsson, already referred to). The local species that are thus made out of the wide-ranger are more closely related to it than to others, and the whole goes to show the truth of Guppy’s deductions as to the breaking up of the widely ranging species into local forms—the process of differentiation. As I have said (28, p. 135), “isolation, *as isolation*, favors the production of new forms.” It is impossible for me to go over every one of the thousands of species with which I deal, to determine its latest systematic position; one is reminded of the Scarabee’s remark, “Cuvier had to go to Latreille for his insects, and if Latreille had been able to consult me—yes, me, gentlemen⁵ he wouldn’t have made the blunders he did about some of the coleoptera.” My opponents treat statistics in a very cavalier way. I say that statistics show for example that the average Scot is heavier than the average Englishman, and they reply in effect “Oh that’s absurd, for here is Smith weighing 180 pounds and McKenzie only 140.”⁶

RECENT PAPERS

A considerable number of papers, in favor of, or opposed to, Age and Area, have been published during the last few years, and it will be well in conclusion to deal with some of these, as illustrating points that have not been dealt with in the general reply to objections that has been made above.

My views are sometimes objected to, on the ground that they seem to imply that the number of species is tending to increase rather than to remain constant, and it is therefore of interest to find that G. R. Wieland, in the fifth chapter of “Organic Adaptation to Environment” (Yale University Press, 1924) shows that the view which is very frequently put forward, that previous ages have had vast numbers of species, lacks good evidence to rest upon. He points out that as yet only about 12,000 well described species of fossil plants are known. Berry makes the number 20,000, but even this is but small beside the number of living species. Wieland thinks that at the beginning of the Cretaceous 40,000 species of flowering plants may have existed in the world. Only the Pteridophytes and the Gymnosperms, of living classes, have gone down in numbers since the Permo-Trias, and all the rest have increased. He then calculates the rate of evolution from these figures, and comes to the conclusion that one species in 80 years would be sufficient—a figure which offers an interesting comparison with my estimate of one in 50 years, and Mr. Yule’s of one in 15 to 30 years.

Miss Chandler has published some very interesting work upon the geological history of *Stratiotes* (3), showing that it has usually been represented by one species only on each geological horizon. The differences between two successive species are hardly explicable otherwise than by

mutation, and they have no apparent reference to usefulness, proceeding for example from a testa with tubercles in rows to a testa with scattered tubercles, and finally to the existing *S. aloides* with none. It is specially noteworthy, however, that the tubercled and smooth forms of *S. aloides* have been found in the same geological horizon, e.g., from samples of the Cromer Forest Bed at Beeston, and it looks as if they might have been in existence at the same time. The impression one gathers is as if the whole species perhaps changed simultaneously, or nearly so, and as one can see no use-relationships in the characters that have changed, there *may* have been some internal force, of an orthogenetic character, regulating it. In this connection, Hurst's work is of very great interest, and will be mentioned below, while attention should also be drawn to that of Rosa (20, 21), though space will not allow of its detailed consideration. According to him, species change over their whole area, tending to continual dichotomous splitting, one new species being rather progressive, the other the reverse. The "future" open to these species becomes continually less and less as the splitting goes on.

Hurst's work (16) goes far towards an explanation of many things that have always been stumbling blocks, providing a new standard for classification, and showing that the species arise in the genus *Rosa* to a great extent by loss of chromosome septets, each septet carrying with it a considerable number of characters. This indicates that the origin of species one from another by single steps—one of the implications of the hypothesis of Age and Area which is strongly supported by the facts of geographical distribution, and for which I have contended since 1907—is a highly probable event. It also indicates that the origin of the same,

or very similar species, in two widely separated regions, is by no means an impossible event.

Another geological paper which bears on the subject is that of Woodhead (32). The last paragraph states "These studies of the Pennine Peat indicate that the species found at the base, and presumably the oldest in the area, are the same as exist on the moors today; further that they have now the widest distribution, and extend into the Arctic regions. It is suggested that as the Southern Pennines was an unglaciated area during the Ice Age, these moorland species would for the most part persist through that period. As the ice receded, many of these would serve as efficient colonizers and extend their bounds. Maps indicating their distribution in detail, show that they occupy a larger area than any other group of native species. This generalization also applies to the whole county of Yorkshire, thus from a different line of enquiry supporting Willis's contention of Age and Area, that the plants which occupy the greatest area in a given country, at a given time, are the oldest plants in that area."

Important evidence has also been given by Guppy (11), who shows that the Canary Islands display a double endemism, that peculiar to the group (about 400 species), and that which it shares as a member of the Macaronesian region including Madeira, the Azores, and the Cape Verde Is. (about 50 species). On the hypothesis of Age and Area, the latter will be the older, and in actual fact they prove to be what are often called the Tertiary relics of these islands (though by the way they show no signs of dying out), while the former are endemic species of more recent Mediterranean genera. Not only are the Macaronesian endemics distributed outside the Canaries to the other islands mentioned, but also, just like the

Ceylon-South-Indian species in Ceylon, they are more widely distributed in the Canaries themselves than the younger endemics of Mediterranean forms, occurring on an average in 3.5 islands each, while the latter only occur in 1.7.

He quotes Pitard and Proust as describing the origin of species from the widely ranging polymorphous species: e.g., *Micromeria varia* occurs all over the islands, while there are 15 endemic *Micromeris* confined to one, 3 to two, and 1 to three islands. He quotes my paper of 1907 (26) in this connection.

Dr. Willey (24) gives an interesting table showing the frequency in capture by townet in the Gulf of Guinea of those Copepods found only there (average frequency 1.8) and those that also occur in the Great Acadian Bight (average frequency 51.7, lowest 5, highest 106). He also finds some evidence of the theory developed by Guppy and adopted by myself that a dominant species of wide range may throw off mutants and continue on its course.

Broekens (1) has carried out a useful piece of work in which Age and Area is put to a test which it may legitimately be supposed to bear, and where it is used in conjunction with morphology and with other lines of work. Taking a middle line with the comprehensiveness of the genera, he finds that the family Onagraceae contains 10 monotypic genera, all confined to warm America, as are also the 7 genera with 3 to 6 species. Taking size of genera as well as area occupied and working with 17 genera, all these therefore may be supposed to be young. There remain 11 genera; of these *Circaea* (7 spp.) is widely distributed through the North Temperate Zone (Europe, Asia, America). *Boissduvalia* (8) is confined to California, Peru, and Chile, and is thus probably younger, though it is not safe of course to

draw conclusions from single cases. *Lopezia* (12), confined to Central America, is pretty certainly younger, and probably *Chamissonia* (15) in the United States, Peru, and Chile. Next come *Gaura* and *Goderia* (each 20) chiefly confined to Mexico or California, and therefore quite probably young, whilst *Ludwigia* (20) is cosmopolitan, and therefore probably old. The last four genera are *Jussieuia* (40, or if united to *Ludwigia*, as is often done, 60), cosmopolitan in warm countries, and with one species, *J. suffruticosa*, almost covering the generic range; *Fuchsia* (60) in America with a subgenus in New Zealand, and therefore probably also old; *Epilobium* (160), cosmopolitan in temperate and cold regions, with some species of enormous distribution; and *Oenothera* (52), confined to America, and therefore quite probably comparatively young.

From these an application of Age and Area (noting however that one is working with single genera to some extent, which is somewhat risky) picks out the group *Jussieuia*, *Ludwigia*, *Epilobium*, and *Circaea* as probably the oldest. All the others, except *Fuchsia*, are confined to America.

Applying next the morphological characters and structure, for example the length of the calyx-tube, he obtains confirmatory evidence that points to *Jussieuia* as the oldest genus, especially when *Ludwigia*, which has as primitive characters in many respects, is united to it. Into the further details of this interesting paper we cannot go, but it requires special mention as a good example of work in which Age and Area is temperately used.

Following the general lines of my work upon the various invasions of New Zealand by plants, Matthews (17, 18) has begun a series of papers upon the British flora. Dealing first with the flora of Perthshire, he points out how the various species show graduation into progressive

arithmetical series, like the flora of New Zealand. At the first glance, they do not seem very regular, but if one separates the alpins from the lowland plants, this difficulty disappears. There are no endemics of course in Scotland, but the figures show their chief concentration at the mouth of the Tay, and it is up that valley that the invasion of the Highlands by Southern forms has proceeded. In later papers he deals with the British flora as a whole, taking in the first the 266 plants confined to England and Wales. These are found to diminish from the southeast in all directions north and west, and the figures become much more regular when divided into four groups, which show their maxima at the mouths of the Ouse and Thames valleys, near to Southampton Water, and in the peninsula of Cornwall. As Mrs. Reid puts it, "Mr. Matthews has proved that though Age and Area on the surface appears to hold not particularly well, it is not because it really fails, but because it is masked by a disturbing cause, and when that cause is discriminated and eliminated, there stands the law fully evidenced."

Matthews' second paper deals with the plants of England, Wales, and Scotland only, and he shows that the southern, non-alpine, forms have advanced in the same way as those of the previous paper, but further, whilst it is no longer possible to determine in detail the number of directions in which they invaded.

Fernald (5) shows that the unglaciated areas of Gaspé and western Newfoundland bear a considerable number of species which are most nearly related to plants of the western Cordillera, Alaska, and Siberia, though separated from them by about 2000 miles. Of these 225 species some 80 are endemic, a large number for a region in latitude 48°N., though small in comparison to the numbers that occur in

places of similar or smaller size in more southern regions (Canaries 450, Ceylon 790, Cuba 1000, San Domingo 1050, New Zealand 1200, etc). They show a vastly greater endemism than do the plants, largely of Arctic origin, which have come up into the glaciated regions since the retreat of the ice; a fact which points to their much greater age. They have probably persisted in their present location since preglacial times. In spite of their great age, however, the areas that they occupy are very small, and we are invited to consider this as an exception to Age and Area. But the fact of their extreme localization only goes to show that their rate of dispersal is *very* slow, even if not all but entirely held up by the barrier formed by the change of climate that has occurred. One cannot, as required by Age and Area, add these species together in groups of ten close allies, for they largely belong to different and scattered genera, nor can one easily compare them with other groups, closely allied to the first. They are relics, in general divorced from the associations to which they once belonged, and therefore will find distribution a matter of great slowness and difficulty, while in view of the desiccation that has gone on over so much of the continent it is probable that they are hemmed in by ecological barriers at no great distance, if indeed these barriers are not actually closing in upon them, and exterminating them slowly but surely, just as appears to be happening with *Sequoia*, *Cupressus macrocarpa*, and other plants.

To turn to the last critical paper that I have seen, that of Fernald (6), the first criticism that he makes compares the areas occupied by Dipterocarp trees with those occupied by Conifers, and I have already pointed out that as these groups are quite unrelated they cannot be compared. He then goes on to object because

my statements are taken from books rather than from field work. In general the authors of floras enter the localities of their species, and it is obviously impossible for me to verify them for myself, when I am dealing with thousands of species. If by the constant collection of rarities rather than of common species, the former are made to appear more common than they should, it is surely very remarkable that the Ceylon edemics should still be of a rarity of 3.4 (*cf.* above) against 2.1 for the wides, the New Zealand 3.4 against 1.5 for the wides that also reach the outlying islands.

Knowing by long experience the great divergences of opinion as to the standing of this or that form in specific or generic rank, I have never attempted any criticism of the species with which I have dealt, and any criticism directed against me upon these grounds (and there is a great deal) should be directed against the authors of the floras which I have used. If I criticize one species, I must criticise all, and lifetimes would not suffice, nor would anyone admit that my criticisms were justified. Further, I have pointed out above that species-splitting (I have always followed the general lines of Linnean species set by Sir Joseph Hooker) really lends great support to Age and Area.

Another criticism refers to the work of Prof. James Small, and the latter informs me that, as indeed is clear in his article, he did *not* employ Age and Area in his selection of the Andean region for the origin of the Composites, but his own cartographic method (*cf.* his "Origin and Development of the Compositae" pp. 246-7, 250-51, 257, and *Carpolithus hyoseritiformis* Berry).

The criticism of my use of such papers as those of Taylor upon the endemics of New York is answered by what I have said above, that I exercise no criticism

upon what I use. The two families that I have myself studied in the field, giving long periods of time to each species, give very strong evidence in favor of Age and Area, as I have shown (AA, p. 92), and hope to show in more detail in later papers.

In dealing with sizes of genera, Prof. Fernald takes them in a miscellaneous way, and does not compare them each in groups with groups of close relatives, and is again attempting to apply statistical methods to individual cases. If in the world at large six closely allied genera occupy areas (*or* have numbers of species) represented by 10, 8, 8, 6, 4, 3, and six more, closely allied to the first six, by 7, 7, 6, 6, 5, 5, and yet another six, closely allied to both, by 6, 5, 4, 4, 3, 3, then the total areas (*or* species) will be 39, 36, and 25. From these results I should say that it was quite impossible to decide which of the first two *groups as a whole* was the older, but that both were with some probability older than the third, though six is a somewhat small number to work with. It is quite impossible, however, to place individual genera in order of age, or to compare any genera except with their *closest relatives*. The rules of Age and Area &c cannot be indiscriminately applied, and applied *alone*; they must be used along with all other possible evidence. We know so little about the evolution and distribution of plants that we cannot afford to neglect anything that may help in elucidation. When one comes to a genus like *Carex*, so overwhelmingly larger than its most closely related forms, one is naturally tempted to infer that it may be older than they, but when one adds it to a few close relatives, one does not feel so sure. Taking figures from *Die Natürliche Pflanzenfamilien*, one finds the six Cariceae to average 90 species each, the six Sclerieae 18, the six Hoppieae 5, the

four Gahniae 17, and the sixteen Rhynchosporae 20. From these figures one feels inclined to say that the Cariceae are *as a whole* the oldest group, and one must then go on to take the areas occupied, when one again finds them on the average covering the largest areas. But out of the many Rhynchosporae one can pick as many and as widely distributed genera as the whole of the Cariceae, so that in the end one is led to the conclusion that the Cariceae are probably *as a whole* the oldest of the smaller groups, leaving the Rhynchosporae out of consideration. But more probably the latter are really more nearly allied to the smaller groups than are the Cariceae, so that it is rather the latter that one should leave out of consideration, looking upon the Rhynchosporae as not improbably the oldest, as a whole, of the remaining groups. And one must go on to apply all the resources of taxonomy, palaeontology, cytology, and the rest, to the question.

With regard to the protean genera like *Rosa*, the explanation seems to me to lie, with great probability, in Hurst's work upon this genus (16). If confirmed by work upon other similar genera, this work will create a wholly new outlook upon the problems of geographical distribution, while at the same time it affords strong evidence in favour of some of the implications of Age and Area, which are probably one of the reasons why it is looked upon by so many with disfavor. For example, take the differentiation hypothesis, as it has been outlined by Huxley (15), and more fully elaborated by Guppy in various books and papers (especially 12, 13, and 10), postulating a primitive type widely ranging in days when the surface of the earth and the climates were more uniform, and then differentiating, with the differentiation of climates that has gone on, into many other genera and

species whose range is less wide, as their age is less great. In some cases the original genus, or something very like it, seems to survive, as with *Senecio* in the Compositae (AA, p. 172), but sometimes it has become broken up as in Monimiaceae. But this whole subject will probably require great revision by aid of cytological investigation. The primary differentiation of *Rosa*, and its adaptation to more differentiation of climates, seems to go hand in hand with the loss of septets of chromosomes, each septet largely carrying with it adaptability to some particular climatic conditions. Hurst's map of the distribution of diploid and polyploid species is very instructive in this connection, showing the greater ranges of the older polyploid species, and the detailed work promised will be looked for with great interest. Incidentally this work also goes to show that it is by no means impossible that the same species—as far as chromosome characters are concerned—might at times arise independently on each of the great land masses, though Dr. Hurst informs me that he thinks that only very rarely indeed would the two be absolutely identical. They would usually be separated as taxonomic species or varieties.

SWAMPING AND DYING OUT

One of the most puzzling problems before us is why so many genera are represented in islands and other isolated spots by endemics only. Within the limits at my disposal, it is not possible to deal fully with this question, which requires a paper to itself. Extermination of the more widely distributed form that was presumably the first to arrive, by dying out or crossing, as suggested by Sinnott, will hardly serve as a general explanation. It is doubtless a parallel case to the presence of so many endemics on isolated mountain tops. In the younger islands, more espe-

cially, the genus is often represented by one endemic only, while in older islands there are often a number, usually closely related, and probably derived from the first. Age therefore, as well as isolation, is evidently a factor in the problem. Miss Chandler's observations on the succession of forms in *Stratiotes* doubtless will come in here, as well as Hurst's work on *Rosa*, and other papers. The problem must remain for the present unsolved.

Another very moot point is the dying out of species. Because I have said that the Age and Area figures give no evidence of dying out, I have been accused of saying that no species die out—a statement flatly contradicted by fossil evidence. Mr. Udney Yule informs me that the result of a probable *average* dying out would be to leave my figures much as they are, with a tendency to pile up at the lower end—a tendency which they do perhaps show already. Miss Chandler's work above mentioned shows how one species may succeed another, and the appearance of endemics only in so many genera in islands &c shows how a species may probably die out in a given neighborhood by a single (or series) mutation. De Vries, in a recent paper (4) has made an incisive study of this question, and Mrs. Arber and others have also dealt with it. Space will not permit of full discussion, but I am rather inclined to think that a comparatively local species may often be killed out in various ways, while a widely distributed species will tend to mutate to local species and varieties. Hurst's work may throw light upon the whole question.

I have sketched this article hastily in response to a request, as for the next few months my editorial and teaching duties will occupy all my time; and there is very much more that might be said, and many criticisms that are left unanswered. In general it seems to me that the objections to Age and Area arise (a) from the expectation of a large return for little work, and of a return from Age and Area *alone*, without the assistance of all other lines of work that are available to provide evidence; (b) from the misunderstanding of what statistics, or quantitative data, really are, and their consequent misuse by application to single cases, or their great complication by being applied to unallied forms, and (c) from a more or less complete ignoring of my provisos about reasonably constant conditions, the use of groups of allied species only, comparison between close allies only, the effects of barriers, and the rest. I have tried to insist upon these upon every possible occasion in my book, but for reasons of space, and the great expense of publication in post-war days, have had to leave comparatively untouched the other disciplines about which I have spoken above. Geographical botany is about the most backward section of our science at the present time, but one may wait too long if one wait till the systematists have arrived at agreement about the exact systematic standing and geographical range of every form, in these days when man is so rapidly transforming the earth, and breaking up the old associations of plants.

LIST OF LITERATURE

- AA. Age and Area, Cambridge, 1922.
- (1) BROECKENS, D. J. Ueber den Stammbaum der Onagraceae. *Rec. des trav. bot. néerland.* xxi, 1924, p. 383.
 - (2) CALVERT, P. P. The geographical distribution of insects, and the age and area hypothesis. *Amer. Nat.* lvii, 1923, p. 218.
 - (3) CHANDLER, MISS M. E. J. The geological history of the genus *Stratiotes*; an account of the evolutionary changes which have occurred . . . during tertiary and quaternary times. *Q. J. Geol. Soc.* lxxix, 1923, p. 117.
 - (4) DE VRIES, H. *Scientia*, Dec. 1924.
 - (5) FERNALD, M. L. Persistence of plants in unglaciated areas of boreal America. *Mém. Amer. Acad.* xv, 1925, p. 241.
 - (6) FERNALD, M. L. The Antiquity and Dispersal of Vascular Plants. *Quart. Rev. Biol.* i, 1926, p. 212.
 - (7) GLIBSON, H. A. Age and Area from the viewpoint of phytogeography. *Amer. Journ. Bot.* xi, 1924, p. 541.
 - (8) GOOD, R. D'O. The past and present distribution of the Magnoliaceae. *Ann. Bot.* xxxix, 1925, p. 409.
 - (9) GRISEDACH, A. Ueber d. Vegetationslinien des nordwestlichen Deutschlands. *Göttinger Studien*, 1847. Cf. e.g. p. 562, *Euphorbia Cyparissias*.
 - (10) GUPPY, H. B. Plant distribution from the standpoint of an idealist. *Journ. Linn. Soc. Bot.* xlv, 1919, p. 439.
 - (11) ———. The testimony of the endemic species of the Canary Islands in favour of the Age and Area theory. *Ann. Bot.* 35, 1921, p. 513.
 - (12) ———. Observations of a Naturalist in the Pacific. London, 1906.
 - (13) ———. Plants, Seeds, and Currents in the West Indies and Azores. London, 1917.
 - (14) HOOKER, J. D. Botany of the Voyage . . . Ercebus and Terror, 1853-60.
 - (15) HUXLEY, T. H. The Gentians. . . . *Journ. Linn. Soc.* xxiv, 1888, p. 101.
 - (16) HURST, C. C. Chromosomes and characters in *Rosa*, and their significance in the origin of species. *Expts. in Genetics*, Cambridge, 1925, chap. xxxviii.
 - (17) MATTHEWS, J. R. The distribution of plants in Perthshire in relation to Age and Area. *Ann. Bot.* xxxvi, 1922, p. 321.
 - (18) MATTHEWS, J. R. The distribution of certain portions of the British Flora. I. *Ann. Bot.* xxxvii, 1923, p. 277. II. *Ann. Bot.* xxxviii, 1924, p. 707.
 - (19) PALMGREN, A. Die Entfernung als Pflanzen-geographischer Faktor. *Acta Soc. Fauna et Flora Fennica*, xlix, 1921, p. 1.
 - (20) ROSA, D. Ologenesi; nuova teoria dell' Evoluzione e della Distribuzione Geographica dei viventi. Firenze, 1918.
 - (21) ———. Qu'est ce que l'Hologenese? *Scientia*, Feb., 1923, p. 113.
 - (22) SAMURLISSON, G. Ueb. d. Verbreitung einiger endemischer Pflanzen. *Arkiv. for Bot.* 9, no. 12, 1910.
 - (23) WETTSTEIN, R. VON. Die europ. Arten der Gatt. *Gentiana* aus der Section *Endotricha*, Froel. *Denkschr. Akad. Wien*, 46.
 - (24) WILLEY, A. Ecology and the partition of biology. Presid. Addr. R. S. Canada. *Trans. R. S. Can.* III, xvii, 1923.
 - (25) WILLIS, J. C. Age and Area; a reply to criticism. *Ann. Bot.* xxxvii, 1923, p. 193.
 - (26) ———. Some evidence against the theory of . . . natural selection of infinitesimal variations. *Ann. R. B. G. Perad.* iv, 1907, p. 1, and continuation on p. 17.
 - (27) ———. The flora of Ritigala, a study in endemism. *Do.* iii, 1906, p. 271.
 - (28) ———. The floras of hill tops in Ceylon. *Do.* iv, 1908, p. 131.
 - (29) ———. The geographical distribution of the Dilleniaceae, as illustrating the treatment of this subject on the theory of mutation. *Do.* 1907, p. 69.
 - (30) ———. The origin of species by large, rather than by gradual change, and by Guppy's method of differentiation. *Ann. Bot.* xxxvii, 1923, p. 605.
 - (31) ———, AND YULE, G. UDNY. Some statistics of evolution and geographical distribution in plants and animals, and their significance. *Nature*, 109, 9 Feb., 1922, p. 177.
 - (32) WOODHEAD, T. W. The age and composition of the Pennine peat. *Journ. Bot.*, 1924, p. 301.
 - (33) YULE, G. UDNY. A mathematical theory of evolution, based upon the conclusions of . . Willis. *Phil. Trans.* B 213, 1924, p. 21.



THE PRODUCTIVITY OF LAKES

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FROM the practical standpoint the most important consideration in regard to a lake is its capacity to produce fish, and this is the ultimate aim of all limnological studies. This problem has been attacked from many angles, and a sufficient amount of data on the hydrography, character of bottom, inshore vegetation, phytoplankton and zooplankton and their quantitative determination, as well as their chemical analysis, and on the food of various species of fishes, has now been obtained to render a survey of this field useful. The utility of such a survey is twofold; firstly, to see if there is any single characteristic which can be used as an index of the productivity of a lake, so that this index-characteristic may be tested and its validity confirmed or disproved, and secondly, to see what are the chief deficiencies in our knowledge of the ecology of lakes, so that investigations with the specific aim of supplying the lacking information may be undertaken.

A lake, like every ecological habitat, is a complex of factors, and the productivity of a lake will obviously depend upon the summation of these factors. For this reason the investigation of every limnological factor is of value. It is not necessary for the purpose of this brief paper to discuss all these factors in detail, but it should be clearly stated that nothing which is said in this paper is to be construed as minimizing the value of the very

fullest investigation of all the factors of a lake.

An examination of the literature dealing with the productivity of bodies of water reveals a strong tendency in recent years to correlate productivity with the amount of plankton. This is but natural, seeing that the great majority of young fishes, and many fishes throughout their lives, feed on planktonic animals, especially on Entomostraca. The second tendency is to seek to relate productivity to the development of organic detritus on the bottom (Petersen and Jensen, 1911; Adamstone, 1924). Some authors, following the lead of Putter (1909 *et seq.*), have sought to prove that the nutrition of many aquatic animals, including fish, depends, at least to a considerable extent, upon organic substances dissolved in the water. Naumann (1918 and 1921) believes that the chief nutriment of many planktonic animals (Cladocera, Copepoda, Rotatoria) consists of the "seston" or fine organic particles suspended in the water.

It will be seen, however, upon close analysis, that none of the above really get to the bottom of the problem of productivity. In the case of the phytoplankton it is true that a large part of the nutriment they yield is elaborated from carbon dioxide and water by photosynthesis, and it is equally true that the supplies of these two materials, are universally present in water, and the energy (sunlight) used in their transformation to sugars and starch

is likewise universally available. Therefore if the development of phytoplankton depended solely on these factors it should be equally abundant in all waters,—which is not true. It is quite evident that there is some factor which limits the production of phytoplankton, and this factor is undoubtedly the availability of elements which are necessary for the formation of protoplasm, especially nitrogen and phosphorus. In the case of organic compounds, whether present as detritus, or seston, or dissolved in the water, it is quite evident that they are secondary products, and that the manner of their production must be explained if we are to arrive at the ultimate factors in the productivity of lakes.

There is, here and there, in the literature, a suggestion that the rooted aquatic plants play an important part in the productivity of bodies of fresh water. I was led to make a survey of such literature as I had at hand, with this point in mind, by my observations, firstly, that entomostracans were most abundant both as to species and individuals, amid the rooted vegetation of lakes, secondly, that other aquatic invertebrates (protozoans, rotifers, amphipods, isopods, mollusks, insect larvæ, etc.) were abundant in such habitats, and, thirdly, that lakes in which I have found an extensive development of rooted vegetation, such as Lake Opinacon, and Burford Lake, were renowned resorts of the angler.

Before giving a brief review of the literature on the rôle of rooted aquatic vegetation it may be well to summarize the various points in connection with the part they play in the economy of lakes.

1. Rooted aquatics, such as *Elodea*, *Potamogeton*, *Vallisneria*, *Myriophyllum*, *Najas*, *Nymphaea*, *Castalia*, *Brassenia*, *Nymphaoides*, *Sagittaria*, *Ranunculus aquatilis*,

Bidens beckii, *Lobelia dortmanna*, *Polygonum amphibium*, *Eriocaulon septangulare*, etc., absorb salts, including nitrates, phosphates and potassium compounds, from the soil (Pond, 1905). When they decay these salts are added to the water, where they are available for the use of phytoplankton.

2. These plants, on decay, add organic compounds to the water, and, as has been demonstrated by Artari, Knorrich, Snow, and myself, organic matter in solution augments the growth of planktonic green algæ.

3. These plants, on decay, contribute very materially to the organic detritus, which not only favors the growth of more plants, but forms the chief food of many aquatic animals.

4. They provide places of attachment for immense numbers of algæ (Chlorophyceæ, Cyanophyceæ, Diatomaceæ), which form the food of many aquatic invertebrates.

5. They provide places of attachment for the eggs of various species of animals.

6. They serve as forage plants for some aquatic animals, such as some insect larvæ (Moore, 1913) and amphipods (Embrey, 1912).

7. They provide hiding-places for fish.

8. They tend to hold the soil of the bottom, including the organic detritus, in place, thus keeping it from being carried into water too deep for the growth of rooted plants.

There are two other rôles which are often mentioned in considerations of these plants, and which are sometimes regarded as of great importance, but which I am inclined to regard as negligible in the case of lakes. These are, firstly, that they, by photosynthetic activity, add oxygen to the water. This is, unquestionably, an important rôle in the case of aquaria, and

it may be in the case of small, shallow ponds, but in the case of lakes the water, down to the depths at which such plants grow, is sufficiently oxygenated, chiefly by wind action, to provide for the oxygen requirements of any animals which live in such habitats. The second of these rôles is that "they shelter fish from the heat of the sun." This is, I consider, an imaginary rôle, derived from an analogy to conditions on land, as our studies of the penetration of long-wave-length radiation into water tend to refute this contention.

Of the points mentioned above I consider the first four to be by far the most important, as these phases influence, not merely the local habitat, but the whole body of water.

The following survey of literature on this subject is by no means complete, but the material presented is fairly representative, especially as far as North America is concerned.

Thompson (1896) says that "The flora of Pine Lake is exceedingly meager. The observer may row along its shore for miles without seeing one thrifty bed of water-weeds," and Ward (1896) comments on the poverty of the fauna of this lake.

Lemmermann (1897) says "Ausserordentlich wertvoll für die Fischteiche sind dagegen nach meinen Beobachtungen die Pflanzen mit Schwimmblättern, wie *Potamogeton natans*, *P. crispus*, *P. amphibium*, *Hydrocharis morsus ranae*, etc."

Embrey (1912) speaking of fresh-water amphipods, says "All forms were always found associated with vegetation, living or dead."

Moore (1913) shows that many forms of life are associated with the potamogetons, and says that "The present investigation affords further evidence of the economic value of these plants."

Kofoed's statement (1903) that "The

amount of plankton produced by bodies of fresh water is, other things being equal, in some inverse ratio proportional to the amount of its gross aquatic vegetation of the submerged sort" is often quoted, and accepted as it stands. It should be observed that Kofoed was here dealing with *Ceratophyllum demersum*, a non-rooted aquatic which comes into direct competition with the phytoplankton, and not with rooted aquatics which do not so compete for nitrates and other salts.

Galtsoff (1924) says "It has been found that the production of plankton can be considerably increased if the pond is drained and its bottom allowed to overgrow with vegetation. When several months later the pond is again filled with water the zooplankton develops in greater abundance." The only reasonable explanation of this increased productivity lies in the materials furnished by the decaying vegetation, and this statement tends to bear out the contention as to one of the major rôles played by rooted aquatics.

Moore (1920), dealing with the ecology of ponds at the Fairport Fisheries Biological Laboratory, says that in pond 2D "fully one-tenth of the surface has been covered by the large rooted aquatic *Potamogeton illinoensis*," and that this pond produced *Volvox* and *Bosmina* in tremendous numbers, the entomostracan feeding on the *Volvox*. Wilson (1923) says that this same pond, 2D, "contained more than twice as many beetle species as pond 1, and while in the former seven species were abundant and eight were common, in the latter only two abundant and four common." Pond 1D had mats of algæ but no *Potamogeton*. Wilson also states that the *Potamogeton* increased from year to year until it covered one third of the pond, and that "the beetle fauna has steadily increased in number and variety."

Reighard (1913) speaking of the fish communities of Douglas Lake shows that three species are characteristic of the stony shoals, and five species of the deep water, while ten species are characteristic of the submerged vegetation, eight of which are found only amid this vegetation. He also states that two more species—the small-mouthed black bass and the pike—occur at the edge of the vegetation and make frequent forays into it in search of food.

Muttkowski (1918) finds that there is, in Lake Mendota, a far more varied and abundant fauna among the rooted aquatics than in any other habitat.

Baker (1916) says "Plants not only afford a place for support, upon which snails may crawl and find a resting-place, but they are actually eaten as the regular food supply. In view of this fact the statement of Shelford (1913, p. 58) that 'we could probably remove all the larger rooted plants and substitute something else of the same form and texture without greatly affecting the conditions of life in the water, that is, so far as the life habits of the animals are concerned' is misleading."

Baker (1918) under the heading "Submerged Vegetation" says "When it is remembered that each plant harbors a host of animals (mollusks, crustaceans, worms, insects, etc.) it is at once apparent that this abundant plant life forms a primary food supply of great value," and "The greatest development of plant and animal life on the bottom is found within the six-foot contour. Of the 1,164 acres examined about 88 per cent of the individual invertebrate animals were found within the six-foot contour. . . . When we remember that fish are more abundant within the six-foot contour, where the majority of young fish live and most adult fish breed, the significance of

this richness of bottom life in the shallow water is at once realized, and indicates that this is the most important depth for the culture of fish."

Some idea of the quantities of vegetation produced in lakes may be gained from the work of Rickett (1924) who states that from 0.25 of a square metre in Green Lake, Wisc., 2,700 grams (wet weight) of submerged aquatics were obtained.

Needham (1922) speaking of submerged aquatics in Lake George, N. Y., says "In this rich mixture of weeds a very great number of small crustaceans, insects, mollusks, and worms, find food and shelter. They in turn furnish food for fishes."

Adamstone (1923) says of Lake Nipigon "As regards animal life, and particularly Mollusca, the most productive parts of the lake are the small sheltered bays and the channels between islands. This is true, especially where the bottom is covered with sand or mud, on which there is much organic debris to furnish food material." The same writer, (1924) recognizes the importance of submerged aquatics, for among his suggestions for increasing the productivity of Lake Nipigon he includes "Since Lake Nipigon so largely lacks aquatic vegetation, amongst which other investigators have found enormous numbers of organisms, it might be possible to introduce species of plants not already found there or to disseminate more widely those which have already established themselves to some extent."

Evermann and Clark (1920) discuss the rôle of aquatic plants as oxygenators, as shade, as protection and as food. They state that "The vegetarian minnows feed upon plants or plant fragments of appreciable size, and the carnivorous forms feed largely on aquatic insects or their larvæ which in turn feed on the plants. The bluegill, which is largely a vegetarian, feeds directly at times upon the leaves of

pond-weeds (*Potamogeton*), and at other times upon the little crustacean, *Asellus*, which feeds upon the weeds."

The most valuable contributions with which I am familiar towards our knowledge of aquatic vegetation have been made by Pearsall, and the value of these papers lies in the fact that he relates the aquatic vegetation not only to the character of the bottom, but the latter to the geological formations in which the lakes are found, and, on the other hand, he relates the vegetation to the fish of the lakes. Pearsall (1920) says "The distribution of the aquatic plants considered is primarily governed by the nature of the substratum, while the reaction of the substratum to vegetation is controlled by variations in the quality and quantity of sediments deposited on it and by the type and quantity of organic matter it contains." The same investigator (1921) says "This detailed discussion shows clearly that the fundamental factor in the development of the attached vegetation is the increase in abundance and richness of the sediments. Not only does this control the types of plant communities found, but it also limits the quantity of vegetation produced." . . . "As a lake develops, silts become richer and more abundant, and *rooted vegetation* more luxuriant. Hence there are increased areas on which epiphytic algæ can grow, and increased shelter and food for the smaller aquatic animals." . . . "It would thus appear that the increase in rooted vegetation, in the bulk of the plankton, and in the abundance of fish, are all changes to be correlated one with another, and ultimately depend upon the topographic development of the lake."

In this latter paper Pearsall touches upon a point in connection with the English Lakes which I have observed in our lakes, that is, that certain fishes are

typical of "non-silted" lakes, for instance trout, and others of "silted" lakes, perch, both here and in England, and black bass in our waters. He is not able to give a satisfactory explanation of the absence of trout from the "silted" or evolved lakes, though he suggests "the silting up of their stony feeding grounds" and "summer stagnation." I would advance, as a tentative suggestion, the competition of the perch, bass, and other predaceous fishes which flourish in evolved lakes. Since this is a most important question in regard to fish culture in North America every effort should be made to arrive at definite conclusions concerning it.

Menzies (1925) states that the young salmon (smolts) grow far more rapidly in silted streams than in rock-bottomed ones, and that their growth rate is correlated with the geology of the region in which they occur.

The aim of this brief paper is, as was stated at the beginning, to see if we could get any suggestions as to an "index character" of the productivity of lakes. It would appear that the amount of rooted submerged vegetation *may* be such an index character, and it would seem to be decidedly worth while to see if this conclusion is valid. If it is, we have here an index character which can be "read" far more easily and quickly than factorial measurements or plankton estimations, and this will be of special value in a country such as ours where inland waters are both numerous and spread over a large territory. Moreover, if it is definitely proved, by quantitative studies, that the rooted aquatics play a major rôle in the productivity of lakes it should be possible to introduce them in suitable places, if any such exist which are not yet occupied by them, or even to change limited areas of bottom, by diminishing wave-action or bringing in soil, so as to render such areas suitable for their development.

LIST OF LITERATURE

- ADAMSTONE, F. B. 1923. The distribution and economic importance of Mollusca in Lake Nipigon. Pub. Ont. Fish. Res. Lab. No. 14.
- . 1924. The distribution and economic importance of the bottom fauna of Lake Nipigon. *Ibid.*, No. 24.
- BAKER, F. C. 1916. The relation of mollusks to fish in Oneida Lake. Tech. Pub. No. 4. N. Y. State Coll. Forestry. Syracuse.
- . 1918. The productivity of invertebrate fish food on the bottom of Oneida Lake. *Ibid.* No. 9.
- EMBODY, G. C. 1912. A preliminary study of the distribution, food and reproductive capacity of some fresh-water amphipods. *Int. Rev. d. ges., Hydrobiol. u. Hydrog. Biol. Sup.* 3.
- EVERMANN, B. W. AND CLARK, H. W. Lake Maxinkuckee. A physical and biological survey. Vol. 2. Pub. of the Ind. Dpt. of Cons., No 7, 1920.
- GALTISOFF, P. S. 1924. Limnological observations in the Upper Mississippi Bul. U. S. Bur. Fish., 39: 347.
- KENDALL, W. C. 1924. The status of fish culture in our inland waters, and the rôle of investigation in the maintenance of fish Resources. Roosevelt Wild Life Bull., Vol. 2, No. 3.
- LEMMERMANN, E. 1897. Resultate einer biolog. Untersuchung der Forellenleiche von Sandfort. *Forschber. Biol. Sta. Plön.*, 5: 104.
- MENZIES. 1925. The Salmon.
- MOORE, E. 1920. Some plants of importance in fish culture. U. S. Bur. Fish. Document No. 881.
- . 1913. The patamogetons in relation to pond culture. Bull. U. S. Bur. Fish., 33: 351.
- MUTTKOWSKI, R. A. 1918. The fauna of Lake Mendota. A qualitative and quantitative study with special reference to the insects Trans. Wisc. Acad. Sc., 19: 374.
- NREDHAM, J. G. 1922. A biological survey of Lake George, N. Y. N. Y. Cons. Comm. Albany.
- PEARSALL, W. H. 1920. The aquatic vegetation of the English lakes. *Jour. Ecology*, 8: 12.
- . 1921. The development of vegetation in the English lakes, considered in relation to the general evolution of glacial lakes and rocks Basins. *Proc. Roy. Soc., B*, 92: 259.
- PETERSEN, C. G. J. AND JENSEN, P. B. 1911 Valuation of Uro Sea. I. Rpt. Danish Biol. Iota., 20: 1.
- POND, R. H. 1905. The biological relation of aquatic plants to the substratum. U. S. Fish. Comm. Rpt. for 1903.
- RICKETT, H. W. 1924. A quantitative study of the larger aquatic plants of Green Lake Wisc. Trans. Wisc. Acad. Sc., 21: 381.
- REIGHARD, J. 1915 An ecological reconnaissance of the fishes of Douglas Lake. Mich. in mid-summer. Bull. U. S. Bur. Fish., 33: 215.
- THOMPSON, H. D. 1896. In a biological examination of Lake Michigan in the Traverse Bay region. Bull. Mich. Fish. Comm. No. 6.
- WARD, H. B. 1896 A biological examination of Lake Michigan in the Traverse Bay region. *Ibid.*
- WILSON, C. B. 1924. Water beetles in relation to pondfish culture. Bull. U. S. Bur. Fish., 39: 231.





NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of THE QUARTERLY REVIEW OF BIOLOGY, 1901 East Madison Street, Baltimore, Maryland, U. S. A.

A STATIC THEORY OF HEREDITY

Being a review of *The Theory of the Gene* by T. H. Morgan. New Haven (Yale University Press), 1926. 6½ x 9½; xvi + 343. \$4.00.

By Julian Huxley, King's College, University of London

The very title of this book provokes to historical reflection. Some biologists have fought against the term *gene* because it recalled Darwin's hypothesis of pangenesis, that edifice of speculation which the great naturalist, as he himself wrote, felt constrained to advance in spite of the absence of any confirmation in fact, because of the imperious need which his mind felt for some intelligible mechanism of what was then the "great mystery" of heredity. Today, not only has the word *gene* come to stay, but Morgan can quite justifiably give his book this proud title, safe in the assurance that the theory of the gene is now as fundamental for biology as is the theory of evolution itself, something which in spite of possible modifications will always have to be reckoned with as an integral part of the science, like the theory of stratigraphical

succession for geology, or the atomic theory for chemistry and physics.

Put in most general terms, a theory of genes implies a particulate theory of life. It implies that the hereditary constitution of organisms is not an indivisible whole, but an organization of units or factors which can be taken apart and recombined in very various ways, in precisely the same way as, on the atomic theory, a chemical compound is not something indivisible, but an organization of units which can be taken apart and recombined in other ways.

There have been a great many other particulate theories of life. But all these were alike in being the purest speculations, incapable of confirmatory test, merely *ad hoc* explanations. Weismann's great edifice of theory comes in a slightly different category. True that his *ids* and determinants were wholly speculative entities; and true that it has turned out that these particular speculations were incorrect. But at least he did attach his speculations to something tangible, by locating his units in the newly-investigated chromosomes; and this guess has proved to enshrine the truth.

Meanwhile Mendel had taken the first step towards the modern theory of the gene. He had demonstrated that, in

certain cases, the inheritance of visible characters depended upon invisible factors, which must be units, must be separable from each other and must behave in a precise and regular way, capable of being prophesied beforehand. On the other hand, he failed (because of technical difficulties which he could not then appreciate) to extend his results to certain other forms. Naudin had also attained very similar results, but not only did he also fail to generalize them, but they were never as clear-cut as Mendel's, and his proof of the existence of unit-factors was never rigorously complete.

There the matter rested for nearly forty years. Bateson was on the verge of discovering the existence of unit-factors for himself, when their existence, in Mendel's work, was re-discovered in 1900. It was characteristic of Bateson that he never dreamt of pressing his claims to independent discovery, but himself became the protagonist of Mendel as the founder of a new branch of science. From that day, only a bare quarter of a century ago, to this, progress has been rapid. Looking back we can see that there have been four or five main advances, each demanding a period of years. It will clarify our perspective to recall them.

First there was the extension of Mendel's ideas to all kinds of organisms and all kinds of organic characters. In this, Bateson was the protagonist, and the second edition of his *Mendel's Principles of Heredity*, published in 1909, may be taken as marking its close. By then it could be clearly seen, by all those with eyes to see, that the existence of hereditary unit-factors was not an isolated or exceptional fact, but was the rule in at least all higher animals and plants.

Arising out of intensive and extensive survey came, as was inevitable, a modification of the original simplicity of Mendel's

two laws. Bateson and Punnett discovered what we now know as linkage. They also discovered mutually-interacting factors, multiple factors, incomplete dominance, reversal of dominance, and other complications.

Meanwhile, quite independently, progress had been made along the line already taken by Weismann of linking on the invisible hereditary factors to the visible machinery of the chromosomes. Sutton very early put forward the view that Mendelian factors were located in particular chromosomes; this was ably defended by numerous other cytologists, particularly in America, but convincing proof was lacking.

The close of the first decade of the twentieth century was marked by notable advances. Johannsen in Denmark clinched Weismann's views on the need for distinguishing between inherited germinal variations and non-inherited somatic variations, by his beautiful analysis of variation in pure lines in beans. Doncaster discovered sex-linked inheritance, and was quick to connect it with the cytological facts concerning sex-chromosomes.

Here closes the second chapter of Mendelism. The next chapters alter the character of the theory itself and inaugurate what we may call neo-Mendelism. The great advances here fall in the second decade of the century. They begin with the discovery of *Drosophila* as an ideal genetic material, and are due chiefly to Morgan, Bridges, Muller and Sturtevant, working in collaboration at Columbia.

The two outstanding achievements of this period are, first the definite and final proof that the chromosomes are the bearers of Mendelian factors; and second that particular factors are situated in particular chromosomes and at particular positions within these chromosomes, so that the

hereditary constitution begins to appear as a set of definite units, arranged in a definite way in space, and existing in definite quantitative proportions. The most spectacular piece of work of this period was the mapping of the chromosomes.

Another great advance of this period was the discovery of hereditary variations due to the subtraction or addition of whole chromosomes, first discovered by Gates, or to the subtraction or addition of whole genomes (complete single sets of chromosomes) as in haploid and polyploid individuals. The most beautiful applications of the first principle have been made by Bridges in his studies of non-disjunction, and of the latter by Wettstein in mosses, while Blakeslee has demonstrated both in operation on the grand scale in *Datura*.

The final great advance concerns the nature and action of factors. This may naturally be subdivided into two more or less separate lines of work, one concerning the relation of factors to other factors, the other concerning their relation to the process of development.

As regards the first, here again the studies of *Drosophila* have been all-important. In the first place came the studies on multiple allelomorphs, which demonstrated that one and the same gene could exist in a whole series of related forms, almost invariably causing a graded series of visible effects. Then came the discovery of true modifying factors, whose visible effects will only be produced if certain other genes are also present to be modified. Most fundamental of all, Bridges was able to prove up to the hilt (what one would have thought was *a priori* to be expected, but was as a matter of fact not generally accepted), that the sex chromosomes exerted their effects not *per se*, or as it were *in vacuo*, but only when

in a certain relation with other chromosomes.

Drosophila, of course, has two similar sex or X chromosomes in the female, an X and a Y in the male. At first it was generally supposed that the X carried the factor for femaleness, the Y that for maleness. Later when the Y chromosome was shown to be without any sex-determining power at all, it was supposed that one X inevitably produced a male, two X's a female. However, Bridges has now conclusively shown that sex-determination is an affair of balance or proportion between X-chromosomes and autosomes; whenever the number of sex-chromosomes is equal to or greater than that of autosomes ($X:A \geq 1$), the type is female; whenever it is equal to or less than one-half that of the autosomes ($X:A \leq 0.5$), the type is male; while when it is about two-thirds of the autosomal number ($X:A = 0.66$), intersexual types are the result. Thus animals with 3 sets of autosomes are female if they have 3 X's, as also are haploid animals with one set of autosomes and one X.

Starting from this point, the extremely fundamental theory of 'genic balance' has been formulated, according to which a gene's effect (quite apart from changes in the environment) depends upon the other genes with which it is connected in the hereditary constitution.

There appear still to be some biologists who attack Mendelism on the ground that it is a preformationist doctrine. There was never much ground for this view: no serious Mendelian ever supposed that a factor was in any way a miniature replica or even representative of a single character. Today there is no ground whatever. The term *unit-character* itself has been almost entirely dropped, for the simple reason that characters cannot be "units;" and we have reached a position precisely

similar to that of the chemists in regard to the atomic composition of matter, or to that of philosophers like Whitehead in regard to the structure of objects in general. The hereditary constitution is not only composed of units in particular proportions and arrangement, but its effects are determined by these proportions and this arrangement just as much as by the particular nature of the units; this standpoint is identical with the chemist's. The properties of water are not those of hydrogen and oxygen added together; but only hydrogen and oxygen combined in a particular proportion will give these properties, while the same elements combined in a different proportion will give hydrogen peroxide, with quite other properties.

A "character" now emerges as the clear-sighted have always seen it—a resultant of a large number of inner agencies, interacting with a large number of outer agencies. The term "unit character" should never have been used, although "unit character-difference" might be permissible.

The great advances of the genetics in the immediate future are thus likely to be in the border area between developmental physiology and genetics in the narrow sense. In this field, the greatest advances have been made outside America, notably by Goldschmidt with his far-reaching work on the genetics and developmental physiology of intersexuality, and Haecker with his "Phänogenetik." *Drosophila* is an unsuitable animal for such studies, owing to its complete metamorphosis and its featureless and inaccessible larva. For this reason, small fish, Crustacea, paurometabolous insects and those whose larvae have abundance of structural features, are likely soon to usurp the centre of the genetic stage. Experiment will become more laborious, since each factor

will have to be examined not for a single final effect, but for the type and rate of change which it produces; and physiology will be able to join hands with pure genetics.

How important such studies are likely to become may be indicated by a couple of examples. Schultz showed that the albino parts of the fur in the Himalayan rabbit and even in some true albinos were not white because of a total absence of some colour-producing gene, but because the threshold for pigment-production could not normally be reached there. If part of the skin be shaved and the animal exposed to cold, the new hairs contain pigment. The normal pigmentation of ears, muzzle, etc. in the Himalayan, is thus apparently an indication, not of a segregation of factors during development, but of a lower temperature in such exposed areas. Again, Ford and myself, working with *Gammarus*, have found that there exist different factors for the deposition of black pigment in the red eye at different rates. The slower the deposition, the later it begins. The deposition caused by one gene only begins after sexual maturity; thus if *Gammarus* were a holometabolous insect, it is probable that this factor would never be able to show any effect! One may also hazard the suggestion that multiple allelomorphs series exert their characteristically graded effects owing mainly to differences in their rates of action.

This review of progress is in large measure a review of Morgan's book: but we may now turn more specifically to its contents and his modes of treatment. In a brief but pithy opening paragraph he stresses the fact, forgotten by some and denied by others (generally those who have not taken the trouble to digest the evidence) that the theory of the gene differs from all other particulate theories of heredity in that previous theories in-

vented speculative units to which any properties could be attached, whereas, in this case, the facts came first, and the very existence of gene-units had to be postulated to fit the data of quantitative experiment.

A straightforward presentment of the laws of Mendel and of linkage is followed by a discussion of their chromosomal basis, with a frank admission that genetics has outrun cytology as regards crossing over (in precisely the same way, it might be pointed out, as cytology at one time outran genetics in regard to sex-determination). An admirable résumé follows of chromosome aberrations in *Drosophila*, which is succeeded later in the book by a whole series of chapters on similar phenomena (including polyploidy) in other organisms. I would draw attention especially to the discussion on *Datura*, on *Oenothera* and on Mosses.

The bulk of the rest of the book is taken up with an account of the determination of sex and the physiology of its development. Chapters on the origin and nature of mutations, an excellent but too brief discussion of species-crosses, a section on gene-stability and some general conclusions complete the volume. The important recent results of botanists in obtaining fertile and stable new forms by crossing distinct species should be studied by every biologist interested in systematics or in evolution.

One or two criticisms may be made. The section on Lamarckism should either have been omitted or else made considerably more exhaustive. As it is, there is no mention in it of the work of Guyer and Smith with rabbits, of Metchnikoff on caterpillars, of Jollos on *Paramecium*, or of Harrison on melanic moths.

In the chapter on sex, the statement concerning Goldschmidt's theory of the origin of intersexuality in *Lymantria* seems

to me somewhat unfair. As is well known, Goldschmidt postulates that a "female intersex" is one which starts existence as a female, but later becomes male, and vice versa: that the precise moment at which the change of sex occurs depends upon the relative "potency" of male-determining and female-determining factors, which in its turn would determine the time at which the effects of one would catch up with those of the other.

Morgan says that this view is bound up with "assumptions concerning enzymes that are philosophical rather than chemical;" and that Goldschmidt's basal assumption, namely that whichever enzyme starts first, is overtaken later by the other, is not a normal feature of enzyme behaviour.

With regard to the latter point, Goldschmidt's "basal assumption" is hardly that ascribed to him by Morgan, but is to the effect that the rate of production of male and female-determining substances is proportional to the potency of the sex-factors.

Quite apart from any such assumptions, however, Goldschmidt's *general* conclusions are as securely based on fact as were Mendel's. It does seem to be definitely a fact that the *Lymantria* intersexes do start life of one sex, and change to the other; that the moment of sex-change varies; and that the precise moment depends upon the balance of two hereditary factors or sets of factors (of which the male-determining is certainly borne in the X chromosome), which can be combined to give whatever results the experimenter chooses. Goldschmidt has, it is true, confused the issue by advancing a number of subsidiary hypotheses which are either unnecessary or even misleading: but this should not detract from his fundamental achievement. This fundamental achievement, as it appears to me, is the correla-

tion of differences between genes with differences between rates of developmental processes.

The Morgan school have practically completed the essentials of what Mendel initiated—a static theory of heredity, concerning the existence and distributions of genetic units. Goldschmidt has here initiated a dynamic view, concerning the relation of genetic units to development, and I venture to say that as time passes we shall come to look on his work as fundamental for this branch of genetic science.

Morgan himself tells us (p. 26) that "the theory of the gene as here formulated, states nothing as to the way in which the genes are connected with the end-product or character," but adds that knowledge of the way in which the genes produce their effects would, no doubt, greatly broaden our ideas relating to heredity and probably make clearer many phenomena that are obscure at present.

It is the more to be regretted that later (p. 32) he speaks of the chromosomes and their behaviour as going "far toward furnishing a mechanism of heredity" when what is really meant is a mechanism for the distribution of hereditary factors. The mechanism of heredity is developmental as well as distributional; and today, more than ever, this needs to be emphasized.

Finally it remains to touch on the evolutionary bearings of the theory of the gene as here set forth. It remains an undoubted fact, which Morgan frankly admits, that the majority of recorded mutations in *Drosophila* and elsewhere are deleterious in their effects. The opponents of Mendelism, of course, seize on this fact and deny all evolutionary significance to mutations, which they dismiss with the epithet "pathological."

Morgan rightly stresses the fact that the

majority of mutations studied by the geneticist are chosen by him because of their striking nature, and that it is likely that striking mutations of large extent will frequently be deleterious; equally rightly he stresses the fact that many small character-differences, often of physiological or biological value have been shown to depend upon inherited unit-factors.

In spite of this there does seem to remain a very real difficulty. In the first place, we are now in a position to assume that every character-difference inherited according to Mendelian principles depends upon a difference between genes in the chromosomes. But we are not yet in a position to assert that all gene-differences owe their *origin* to similar causes. Because white eye in *Drosophila* owes its origin to a single-factor mutation is no reason for supposing necessarily that a Mendelian size-difference found to exist between two races of corn originated in the same way. If Harrison's important work on the induction of melanism in Lepidoptera is confirmed, single-gene mutations may sometimes be induced by specific treatments, as well as originating in an apparently spontaneous way.

We should expect every specific alteration to a chromosomal unit to be inherited in Mendelian fashion: but the alteration might well be brought about in a dozen different ways. Thus in its present condition, the theory of the gene is only knocking at the door of evolutionary theory. Over and over again it demands to be taken into serious account; but it has not yet achieved all that was at one time hoped for from it on the constructive side.

There remains to be mentioned the puzzling but important work of Sumner and his associates on the results of crossing subspecies and local races of mice. The results do not, at first sight, conform with

Mendelian expectation. It is much to be hoped that more work of this nature will be done on natural races. Meanwhile, again, the incompleteness of our evolutionary theory is revealed. One positive point is interesting. Neo-Mendelism is coming round to lay greater and greater stress upon the evolutionary importance of small variations, thereby coming into agreement with systematic zoology and paleontology. It may be that with further analysis the antinomy between "mutation" and "continuous

variation" will be shown to have rested on utterly false bases!

Meanwhile, apart from all such bearings, developmental and evolutionary, Neo-Mendelism has provided biology with a vast body of important facts and with tested theories of fundamental importance, and has been the method of familiarizing biologists with the necessity for rigorous, quantitative experiment. It is an achievement to be proud of: and its main lines are ably and interestingly set forth in Morgan's lucid book.

BRIEF NOTICES

EVOLUTION

THE MECHANISM AND MEANING OF LIFE. *Showing How Death Is Humanity's Crime Against the Individual, and Involving Evolution and the Immaculate Conception.*

By Granville Gates with the collaboration of Anne Williams Gates.

Frederick H. Hitchcock

\$1.50 5 x 7½; 59 New York

The essence of this contribution to The Higher Spiritual Biometry seems to be that "the man who fell by assuming two motives unequal in effect divided himself by two in 'spirit,' actinic power, 'will,' thought or mental action (man and woman); by three in 'mind,' decision, dynamic power or physical action (man, woman and child) and by four in 'body,' static power, potential or physical result (man, woman, child and humanity). Thus humanity is Fallen Man as a mental-physical whole whose past is woman or unconscious or physical diversity of 'sex' and whose future is in the perfection of child or the mental or conscious uniting of 'sex.'

"The following therefore seems to express the full 'sex' or family relation:

Woman = 0.222 (Mental) (Individual woman)

Child = 0.111 (Physical) (Individual man)

Imperfect Man = 0.333 (Mental) (Collective man)

Humanity = 0.666 (Physical) (Collective woman)

*Fallen Man

as a Whole = 0.999 (Mental-physical)

"Humanity is therefore the predominating and relatively inert constant ('666') which retards the reversion of its individuals to instantaneous functional equality." (P. 30.)

From these data the following somewhat startling conclusion is reached: "The period of a woman's true maturity from 22.2 to 33.3 years may be said to be the perfectly voluntary or Christ child period. *In this period the immaculate conception should be relatively easy physically and fairly easy mentally.*" (P. 33.) (Our italics.)



THE GIST OF EVOLUTION.

By Horatio H. Newman. The Macmillan Co. \$1.50 5½ x 7½; ix + 154 New York

A tract of the times engendered by the Scopes trial at Dayton, Tennessee. Chapter III to XII (the end of the book) deal

with purely biological matters and furnish an excellent, brief, popular review of our present knowledge of organic evolution. The first two chapters devote themselves to philosophy and theology, with less happy results. We think that some of our more philosophically minded readers may be entertained by the following quotation (see page 20): "It is deeply to be regretted that the enemies of science have tried to convince their hearers that science and religion are irreconcilable. This cannot be true, for not only are many men of science genuinely religious, but many theologians and great Christian leaders are in entire accord with the scientific views of the time." And still we hear animadversions on the depth of the philosophy and the precision of the logic of fundamentalists!



GENETICS

Vacant



GENERAL BIOLOGY

THE NEW NATURAL HISTORY. *Volume I.*

By J. Arthur Thomson. G. P. Putnam's Sons
\$6.00 8 x 10½; 388 New York

Perhaps there is a subtle and recondite plan behind the arrangement of the material in the first volume of this magnificent, new, popular natural history, but if so it has been concealed with uncanny skill. The reader *seems* to be led about in an entirely casual and haphazard fashion among the wonders of animate nature. The very casualness of the sudden transitions from gorillas to ants, or from squids to spiders, undoubtedly adds to the charm of the book for the general reader. In his

foreword Professor Thomson states that he has been led in this work "to treat of animals not only as threads in a quivering web of life, but as personalities of a sort, which seek after well-being, which even share in their own further evolution. And in this last word the keynote of our New Natural History is sounded, for, without formal discussion of difficult questions, we have sought to illustrate the biggest fact of all, that Animate Nature is a drama still going on." As was to be expected from the author's past performances, the book is charmingly written and beautifully illustrated, mostly from photographs. Altogether the book is an achievement. It should certainly be in every home where there are children. We know of no book on natural history half so thrillingly interesting or so casually unsystematic in its arrangement.

PATHOGENESIS.

By Carl F. Jickeli. R. Friedländer und Sohn
15 marks 6½ x 10; xv + 335 (paper) Berlin

A philosophical contribution to theoretical biology by a man who has never been a professor, but instead appears to have spent his life in the practice of medicine in a small town far from scientific centers. Whether there is any causal connection or not, there certainly seems to be a correlational association between this fact and a certain freshness and novelty in his discussion. The main tenets of the author's faith are two concepts; one of the incompleteness of metabolism, and the other of a principle of organic stability. Starting from these bases he synthesizes a general philosophy of all biological phenomena, but pays especial attention to the origin of disease. The book seems to be of no great importance, but contains a number of ideas of

real interest and originality. The author's knowledge of the literature of general biology is extensive, but spotty.



DIE GESCHICHTE DER BIOLOGIE.

Ein Überblick.

By Erik Nordenskiöld. Gustav Fischer
25 marks $6\frac{1}{4} \times 9\frac{1}{8}$; vii + 648 (paper) Jena.

There has long been a need for a comprehensive and systematic history of biology, handled from a modern point of view. This book, which is a German translation of a series of lectures given at the University of Helsingfors in 1916 and 1917, and subsequently published in Swedish, comes nearer to filling this need than any book which has yet appeared. The material is treated in five main divisions: Biology in the classical period and in the Middle Ages; biology during the Renaissance; biology in the seventeenth and eighteenth centuries; biology in the first half of the nineteenth century; development from Darwin to the present time. There is a section on sources and literature and a detailed index. The book would have been improved by illustrations, but as it stands it is a worthy and welcome addition to the literature of the history of science.



JUNGLE ISLAND.

By Warder C. Allee and Marjorie Hill Allee.
Rand McNally and Co.

\$1.00 $5 \times 7\frac{1}{4}$; x + 215 Chicago
"Jungle Island" is Barro Colorado Island in Gatun Lake, in the Panama Canal Zone. This book is intended for children. It may be characterized as a series of more or less entertaining tales about various aspects of tropical nature. It is extensively but unevenly illustrated. The line diagrams are in the main satis-

factory, but some of the photographs are so badly reproduced as to appear merely as black smudges on the page. This seems a great pity, because obviously in many cases the original photographs were excellent. There is a short chapter of suggestions to teachers and a glossary, from which the inquisitive infant may learn that the technical term "buoy" means "A float marking safe channels for ships," and that "fumigate" is "To smoke out bacteria, insects, or large animals." It seems a little unfortunate to have dragged bacteria into this latter definition.



AVORTEMENT ET STÉRILITÉ.

By H. Vignes et G. Barbaro, P. Rinjard, E. Curot and J. Dufrenoy.

Revue de Pathologie Comparée et d'Hygiène Générale
8 francs $6\frac{1}{2} \times 10$; 110 (paper) Paris

This volume reprints four papers presented at a meeting of the Society of Comparative Pathology of Paris on November 10, 1925. The first paper, by H. Vignes and G. Barbaro, discusses the causes and mechanisms of abortion in the human species; the second, by P. Rinjard, deals with the contagious abortion of cattle (Bang's disease); the third, by Ed. Curot, is on the pathogenesis and diagnosis of sterility in domestic animals; the final paper, by J. Dufrenoy, is on sterility in plants. The first paper is the best in the volume, and the last the worst. Apparently M. Dufrenoy has never heard of the brilliant and fundamental work of East on sterility in plants.



LA MORT ET LA BIOLOGIE. *Essais sur la Mort.*

By Henry de Varigny. Félix Alcan
12 francs $4\frac{3}{4} \times 7\frac{1}{2}$; 309 (paper) Paris

A rather comprehensive review of existing knowledge and opinion about the biology of death, life duration, and senescence. Its authorship by the veteran French biologist, Henry de Varigny, insures, on the one hand, its general accuracy as to facts, and, on the other hand, its literary charm, for there are few writers of science for the people anywhere in the world whose literary gift equals that of de Varigny. The book falls in two parts, the first dealing with the various aspects of senescence and death in the lower organisms, and the second with death in the human species. It is an interesting little treatise.



GOETHE'S NATURWISSENSCHAFTLICHESCHRIFTEN. *Band I and Band II*
Insel-Verlag
Leipzig
28 marks

Band I, 885

$4\frac{1}{4} \times 7$; Band II, 698, 31 pp. figures

In these two attractive little volumes, printed on India paper, the major portion of Goethe's writings on natural science are reprinted. The first volume falls into three main divisions—an opening general section, followed by the papers on biology, which are again followed by those on geology. The second volume deals with Goethe's theory of color and color vision.



THE BACTERIOPHAGE AND ITS BEHAVIOR

By F. d'Herelle (Translated by George H. Smith). The Williams & Wilkins Co.
\$8.00 6×9 ; xiv + 629 Baltimore

This detailed technical account of the development of the present understanding of the bacteriophage, by its distinguished discoverer, is a welcome addition to the literature of general biology and im-

munology. The book is divided into three principal parts dealing respectively with the following subjects: The phenomenon of bacteriophagy; The bacteriophage; The behavior of the bacteriophage protobe. There is a bibliography of 647 titles, and detailed author and subject indices. Altogether is an achievement of which the author, the translator, and the publisher may all well be proud.



DAS INDIVIDUALITÄTSPROBLEM UND DIE SUBORDINATION DER ORGANE. (*Ein Beitrag zum Descensus der Keimdrüsen der Säugetiere.*)

By Dr. Armin Müller.

Akademische Verlagsgesellschaft M.B.H.
Marks 3.50 6×9 ; 95 (paper) Leipzig

A highly abstruse contribution to the philosophy of biology. The descent of the mammalian testes and the organization of the central nervous system are taken as examples illustrative of the author's theory of organic pattern and integration.



JOHANNES MÜLLER. *Das Leben des Rheinischen Naturforschers.*

By Wilhelm Haberling.

Akademische Verlagsgesellschaft M.B.H.
22 marks $6\frac{1}{2} \times 9\frac{1}{2}$; 501 (paper) Leipzig

A well arranged and well written biography of a great man, which includes a considerable amount of new material, especially an extensive selection from his letters. It is a valuable addition to the history of science.

HUMAN BIOLOGY

THE NEED FOR EUGENIC REFORM

By Major Leonard Darwin. John Murray
12 shillings $5\frac{1}{2} \times 8\frac{1}{2}$; xvii + 529 London

This is the most extensive treatise on eugenics, intended for the general reader, that has yet appeared. The distinguished author is the son of Charles Darwin, to whose memory this volume is dedicated, and has been for thirteen years the leader of the eugenics movement in England on its popular side, having held during this period the presidency of the Eugenics Education Society, founded by Galton. While the material itself is largely based upon Major Darwin's lectures and addresses in this field, it is not merely a reprint but the whole has been reworked into coherent and unified form. The twenty-seven chapters range over the whole field of topics that have been discussed by eugenicists since the movement was started. As is to be expected, a great deal more space and emphasis is devoted to the negative than to the positive side of the subject. In the present state of knowledge it is much easier to write about race deterioration than it is to tell how to establish in the race desirable qualities. Not all biologists or sociologists or economists will agree with all the positions taken by the author in regard to the many controverted points which are always necessarily to the fore in eugenic discussions, but at the same time specialists in each one of these fields, as well as the general reader for whom the book is intended, will find much in it to stimulate and inform his thought. The book is well indexed.



THE WORSHIP OF NATURE. Vol. I

By Sir James George Frazer.

The Macmillan Company

\$4.00 6 x 8½; xxvi + 672 New York

This treatise by the distinguished author of "The Golden Bough" displays again

his immense and profound learning. The book originated as a series of Gifford Lectures on natural theology at the University of Edinburgh in 1924 and 1925, but in its printed form considerable additional material has been included. The book describes in great detail the manner in which primitive peoples came to personify and worship the Sky, the Earth, and the Sun, as deities capable of influencing human life. The extent and manner of development of this tendency, as well as its social effect, are described for the ancient Aryans (the Vedic Indians, old Persians, Greeks, and Romans). There next follow similar accounts for the ancient Babylonians, Assyrians and Egyptians, the Chinese and Indo-Chinese, and existing primitive races in different parts of the world—India, America, etc. The sources in the literature are extensively and minutely documented. The book is a contribution of first rate importance to cultural anthropology.



MONGREL VIRGINIANS. *The Win Tribe.*

By Arthur H. Estabrook and Ivan E. McDougale. *The Williams & Wilkins Co.*

\$3.00 5 x 7½; 205 Baltimore

In the making of this detailed study of a family group in the Virginia mountains a geneticist and a sociologist have collaborated, with distinctly good results. The Win family tribe is made up of morally and intellectually low grade people, who represent a combination of three divergent racial stocks—white, Indian, and negro. In part at least as a result of social ostracism, there has been much inbreeding in the tribe. The study has been made with great critical care and constitutes a valuable addition to the literature of eugenics. It is particularly unfortunate that a book

of this type, of which a major part is filled with detailed family records, has no index.



KÖRPERMASSE UND KÖRPERPROPORTIONEN DER ISLÄNDER. *Ein Beitrag zur Anthropologie Islands.*
By Guðmundur Hannesson.

\$2.50

Fjelagsprentsmidjan
Reykjavik, Iceland

6 $\frac{3}{8}$ x 10 $\frac{1}{2}$; vii + 254

This is a contribution to the original literature of anthropology of first-rate importance. The author has measured over a thousand male Icelanders of various ages. In addition to the detailed biometric treatment of his measurements, the author reviews all that is known regarding the anthropology of Iceland. He finds the Icelandic race to be predominantly Nordic; tall, slender statures predominate, with comparatively long faces and light eyes. The variability in respect of types is nevertheless great. Short stature, combined with square build, is common. Mixed or dark eyes are not uncommon. He concludes that besides the Nordic, the Alpine race, and probably the Baltic race too, are to be found in Iceland, and very likely also the Mediterranean race, the last having been imported with the colonists from Scotland and Ireland. There is an adequate bibliography, but, unfortunately, no index.



LES VARIATIONS DU CORPS HUMAIN.

By L. Dubreuil-Chambardel.

Ernest Flammarion

10 francs 4 $\frac{3}{4}$ x 7 $\frac{1}{4}$; 250 (paper) Paris

This interesting treatise by the President of the Anthropological Society of Paris discusses in a semi-popular, but authorita-

tive manner, some of the more outstanding facts of human teratology, and to a lesser extent those concerning the normal variations of the human body. The main divisions of the treatment are as follows: The general variations of the body (including such matters as dwarfism, gigantism, etc.); the variations of the trunk; the variations of the head; the variations of the hands and feet; congenital absence of the limbs; variations in the genital organs; variations of the skin. The book is rather fully illustrated in an interesting way but, unfortunately, the reproduction of the illustrations is inadequate.



POPULATION PROBLEMS IN THE UNITED STATES AND CANADA. *An Outgrowth of Papers Presented at the Eighty-Sixth Annual Meeting of the American Statistical Association, December, 1924. (Publications of the Pollak Foundation for Economic Research No. 5)*
Edited by Louis I. Dublin.

Houghton Mifflin Co.

\$4.00 5 $\frac{1}{4}$ x 8; xi + 318 Boston

In this volume, made up of contributions by some twenty odd writers, various phases of population growth, and its connection with natural resources, immigration, and the labor supply, are discussed. As is to be expected in such a work, the contributions are of varying degrees of merit. The papers by Dr. Warren S. Thompson on the natural increase of population, by Prof. Don D. Lescohier on population and agriculture, and by Dr. Aleš Hrdlička on the effects of immigration on the American type, are particularly worthy of mention. Taken as a whole the book is a timely reference work on the population problem. It is attractively printed and well indexed.

EUGENICS AND POLITICS.

By *Ferdinand Canning Scott Schiller*.*Constable and Co., Ltd.*8 s. 6 d. $5\frac{3}{4} \times 8\frac{3}{4}$; xi + 220 *London*

This volume by the brilliant Oxford philosopher reprints a series of essays which he has at various times contributed to journals, principally the *Eugenics Review*. The most entertaining essay in the volume is the fifth, "Plato and Eugenics," which is also the oldest, having been written in 1899. Altogether the volume is a contribution to the lighter literature of eugenics worthy to rank with the writings of Sir Francis Galton himself in the same vein. This is saying a good deal, because in many quarters the propaganda for eugenics has sadly deteriorated in its quality since Galton's death.



DER DILUVIALE MENSCH IN EUROPA.

By *Dr. F. Birkner*. *Verlagsanstalt Tyrolia*
Rm. 5.30 $5\frac{3}{4} \times 8\frac{1}{2}$; 148 (paper) *Innsbruck*

Considering its small size, and therefore necessary omission of all details, this is one of the best accounts of the present knowledge of prehistoric man that has come to our attention. There are 278 illustrations, well reproduced. The material is presented under four main heads, as follows: The material culture of prehistoric man; the culture of prehistoric man in Central Europe; the psychological characteristics of prehistoric man; his structural characteristics. The book closes with a short, but well chosen, bibliography.



A HISTORY OF AGRICULTURE IN EUROPE AND AMERICA.

By *Norman S. B. Gras*. *F. S. Crofts and Co.*\$3.50 $5\frac{1}{2} \times 8\frac{3}{4}$; xxvii + 444 *New York*

A text-book which not only sets forth

in considerable detail the historical facts in regard to agriculture and rural social and economic life in general, but also makes some attempt to elucidate the meaning of these facts in relation to human evolution. It is extensively documented with bibliographic material, contains a detailed index, and is well arranged for teaching purposes. The author is professor of economic history in the University of Minnesota.



LA FAMILLE SYPHILITIQUE ET LA FAMILLE CANCÉREUSE.

By *Dr. Pfeiffer (de Dijon)*. *Norbert Maloine*
1 franc 6×9 ; 22 (paper) *Paris*

This pamphlet maintains the strange thesis that syphilis is the clinical cause of cancer. The author has studied sixty-six families in which cancer has occurred, and holds that it is always accompanied either by the stigmata of hereditary syphilis or the clinical signs of acquired syphilis. The evidence falls something short of completely proving the thesis.



ZOOLOGY

THE ARCTURUS ADVENTURE. *An Account of the New York Zoological Society's First Oceanographic Expedition.*By *William Beebe*. *G. P. Putnam's Sons*
\$6.00 $6\frac{1}{2} \times 9\frac{1}{2}$; xix + 439 *New York*

The author of this book is able to combine business and pleasure more skillfully and successfully than any other scientific man ever known. In reading this gorgeously illustrated and beautifully printed volume there is an intensive impression of Beebe's unfailing joyousness in his work. His attitude towards his science is extraordinarily like that of Benvenuto Cellini towards his art. This

book is easily the best of the author's popular writings. It is essentially a layman's log of the expedition of the *Arcturus*, lavishly outfitted for a general zoological and oceanographic *reconnaissance* in American tropical waters. Whatever scientific results the expedition may have achieved will be separately reported in other publications. In this volume are presented many observations of animal behavior, particularly that of the entertaining mammal, William Beebe.



ANIMAL ECOLOGY.

By A. S. Pearse. McGraw-Hill Book Co.
\$4.00 6 x 9; ix + 417 New York

There has been for some time a need for a systematic treatise on animal ecology. This work has been written to fill this need. After an introductory chapter largely concerned with definitions, the following topics are discussed: Physical and chemical ecological factors; biological factors; succession; animals of the ocean; freshwater animals; terrestrial animals; the relations of animals to plants; the relations of animals to color; intraspecific relations; interspecific relations; the economic relations of ecology. There is an extensive bibliography, arranged alphabetically by authors, covering some thirty pages. Curiously enough, the book contains no illustrations. We believe it to be unique among treatises on ecology in this respect. It is a well written and useful addition to the literature, without being in any sense profound, or particularly original.



BRITISH BIRDS. (Volume III)

By Archibald Thorburn.

Longmans, Green and Co.
\$5.50 6 x 9; x + 169 New York

The first two volumes of this important

work have already been noticed in earlier numbers of *The Quarterly Review of Biology*. The third maintains, and perhaps even surpasses, the high standard of quality set in the other two. Perhaps one reason why the plates seem more beautiful in this volume than in others is that the ducks, pheasants and grouse lend themselves particularly to artistic ends. The 48 plates in this volume illustrate birds belonging to the following orders: *Herodiones*, *Anseres*, *Columbae*, *Pterocletes*, *Gallinae*, *Grallae*, sub-order *Fulicariae*, sub-order *Orides*, and *Limicolae*. The reproductions of Mr. Thorburn's wonderful paintings are superb. He attributes the marked increase in ducks nesting in Britain to better protection through recent game laws. We wonder just how great a part this particular element in the total ecological situation has really played in producing the observed result.



DIE TIERWELT DER NORD- UND OSTSEE. (Lieferung I, II and III)

Edited by G. Grimpe and E. Wagler.

Akademische Verlagsgesellschaft M. B. H.
Lieferung I, 4.80 marks Leipzig

6 x 8½; 79 (paper)

Lieferung II, 4.50 marks

6 x 8½; 72 (paper)

Lieferung III, 7.80 marks

6 x 8½; 100 (paper)

The aim of this new series is to give a comprehensive, fully illustrated account of the fauna of the North Sea and the Baltic, with particular attention to the ecology and biology of the animals living in these waters. It is expected that the work will be completed in about three years and will include, all told, about 120 signatures. The first three parts now at hand deal with the following groups: *Opisthobranchia* and *Pteropoda* by H. Hoff-

man; *Scaphopoda* by T. van Benthem Jutting; *Amphibia* and *Reptilia* by R. Mertens; *Noctiluca* by A. Pratje; *Teleostei* *Physoclisti* and *Heterosomata* by W. Schnakenbeck; *Echiuridae*, *Sipunculidae*, *Priapulidae* by W. Fischer; *Enteropneusta* by C. J. van der Horst; *Pantopoda* by J. Meisenheimer. The illustrations are line cuts in the text and are in the main diagrammatic. So far as may be judged from the present parts the work will be, when completed, a useful reference source.



BATTLES WITH GIANT FISH.

By F. A. Mitchell-Hedges.

Small Maynard Company

\$5.00 6 x 9; 300 Boston

A most entertaining account of the author's adventures during two years of fishing in the Caribbean Sea and the Pacific Ocean. It is abundantly and rather thrillingly illustrated with photographs taken by Lady Richmond Brown, who accompanied the author on his expedition. Throughout the book there is an obvious effort to impregnate the tale with a flavor of scientific research, but actually the only records of any permanent value are of the enormous sizes to which some fish may attain, particularly the cartilaginous fishes (sharks, rays, etc.). There is no need, however, for the reader to be inhibited by any consideration of this book as a scientific treatise. If he will simply regard it as a tale of adventure he will be rewarded by excellent entertainment and some real thrills.



ZOOLOGISCHES WÖRTERBUCH.

By Dr. Erwin Hirsch-Schweigger.

Walter de Gruyter and Co.

26 R. M. $5\frac{1}{2} \times 7\frac{1}{2}$; viii + 628 Berlin

This well illustrated zoological dic-

tionary will be found a valuable addition to any library. The system of cross-referencing is extremely well conceived and carried out to a fineness of detail that we know of in no other technical dictionary. Pronunciations of technical names are indicated by the use of accents. American readers will find some of these indicated pronunciations different from the accustomed usage here. But this is a trivial defect. Altogether we recommend this dictionary highly, especially to high school and college departments with meager library facilities. It is a pity that there is no such work in English.



THE BOOK OF THE RED DEER.

Edited by John Ross.

Simpkin, Marshall, Hamilton, Kent and Co., Ltd.

10 s. 6 d. $8\frac{1}{2} \times 10\frac{1}{2}$; 161 London

This is an entertaining, well produced contribution to the literature of big game hunting. There are twelve chapters contributed by as many different writers. The major portion of the book is devoted to the red deer of Scotland. While written in a popular vein, mammalogists will find a good deal in it of interest. An appendix contains a detailed list of all the deer forests in Scotland, with statements as to area, ownership, etc.



EMPIRE BIG GAME.

Edited by Hugh Gunn.

Simpkin, Marshall, Hamilton, Kent and Co., Ltd.

10 s. 6 d. $8\frac{1}{2} \times 10\frac{1}{2}$; 228 London

This is a companion volume to the one reviewed immediately above, constructed on the same plan, and carrying in some part the same material. Primarily, however, this volume is devoted to the big

game of the outlying parts of the British Empire, including Canada, Newfoundland, Australia, Africa, India, and Malaysia. These are contributed by different authorities on the hunting and wild life of these regions. Both volumes are illustrated with excellent photographs, and may well find a place on the shelves of any library of natural history.



AN ACCOUNT OF THE CRUSTACEA OF NORWAY. *With Short Descriptions and Figures of all the Species. Volumes VIII and IX.*

By G. O. Sars.

Published by The Bergen Museum, Bergen; sold by Alb. Cammermeyers Forlag, Christiania
Vol. VIII, Kr. 15,00;

8 x 11½; 91 (paper)

Vol. IX, Parts 1-12, Kr. 30,00

8 x 11½; 176 (paper)

In Volume VIII of the author's great work on the crustacea of Norway the *Monstrilloida* and *Norodelphyoida* are set up as distinct divisions of the *Copepoda*, and the following families are placed under them and described: *Thaumatosyllidae*, *Monstrillidae*, *Norodelphyidae*, *Doropygidae*, *Bupproriidae*, *Ascidicolidae*, *Botryllophilidae*, *Enterocolidae*.

Volume IX begins an account of the *Ostracoda*, and in the parts so far issued the following families are discussed: *Cyprinidinidae*, *Conchoeciidae*, *Polycopidae*, *Cytherellidae*, *Cypridae*, *Cytheridae*.



MEMÓRIAS DO INSTITUTO DE BUTANTAN. 1925. Tome II—Fascículo Unico. *Contribution à l'étude du venin des araignées*, par les Drs. Vital Brazil et J. Vellard. *Un nouveau genre et deux espèces nouvelles d'araignées de l'état de S. Paulo*, par le Dr. J. Vellard. *Immunisation anti-*

tétanique par la méthode toxoïde-toxine, par le Dr. J. Lemos Monteiro. *Les différentes phases de l'autolyse du "B. anthracis,"* par le Dr. J. Lemos Monteiro. *Immunisation per os contre le bacille de Shiga. Contribution à l'étude du mécanisme de l'immunité*, par le Dr. Eduardo Vaz.

Instituto de Butantan

7 x 10; 119 (paper)

São Paulo, Brazil

The chief general biological interest of this volume lies in the first two memoirs which take up about three-quarters of the space. They deal with the poisonous spiders of Brazil and their venom in a thorough-going, systematic manner. The volume is a welcome addition to the reference shelves of any zoological library.



NOTE D'ORNITHOLOGIE. *Remarques et Observations sur l'Habitat, les Mœurs, la Migration, etc., de la Bécassine Double (Gallinago media Frisch, 1763).*

By Paul Petitclerc.

Éditions Bossard

45 francs

Paris

7¼ x 9½; 89 + 3 plates (paper)

A monographic account of the solitary or double snipe, illustrated with three fine photogravure plates. After a description of the external morphology of the bird, such matters as habits, flight, migration and local distribution are discussed in detail. Finally, to round out this excellent monograph, a section is devoted to the culinary importance of the double snipe, clearly indicating that the author is a gentleman as well as a scholar.



DIE HAUSINSEKTEN UND IHRE BEKÄMPFUNG.

By Max Dingler.

Paul Parey

Rm. 2 5 x 7½; 96 (paper)

Berlin

This little popular treatise on insect

pests of the household, and methods of controlling them, is of precisely the same character as the practical bulletins which the United States Department of Agriculture distributes free to residents of this country.



MANIPULATIONS ZOOLOGIQUES

A l'usage du P. C. N., des Écoles Normales et des Candidats au Brevet supérieur et au Professorat des Écoles Normales.

By Léon Bertin and Amélie Boisselier.

Les Presses Universitaires de France

20 francs 7½ x 9½; x + 335 (paper) Paris

A laboratory manual for a course in zoölogy, roughly corresponding in content and depth to the zoological part of American college courses in general biology plus vertebrate comparative anatomy. It is extensively illustrated, chiefly with schematic diagrams. There is a detailed glossary of technical terms.



DISEASES OF DOMESTICATED BIRDS.

By Archibald R. Ward and Bernard A. Gallagher. *The Macmillan Co.*

\$3.25 6½ x 9½; xii + 333 New York

A practical treatise on poultry pathology, developed along conventional lines, but bringing into the account of each disease the results and observations reported in recent literature. The book is fairly well illustrated and has author and subject indices.



PALAEONTOLOGY. *Invertebrate.*

By Henry Woods. *The Macmillan Co.*

\$3.50 5 x 7½; 424 New York

This is the sixth edition of the well-known introduction to invertebrate palaeontology, first published in 1893. There is a good bibliography and a detailed index.

BOTANY

THE NERVOUS MECHANISM OF PLANTS.

By Sir Jagadis Chunder Bose.

Longmans, Green and Co.

\$6.40 5¾ x 9; xix + 224 New York

If accepted at its face value, the evidence in this volume would be sufficient to establish the author's thesis that there is present in plants a tissue which corresponds in its physiological behavior to the nervous tissue of animals. Just as in his numerous former researches the distinguished Indian botanist, Sir Jagadis Chunder Bose, has brought to the study of the problems dealt with in the present volume rather elaborate and highly sensitive pieces of apparatus of his own devising. The general conclusions reached are as follows: "It can no longer be doubted that plants, at any rate vascular plants, possess a well-defined nervous system.

"It has been demonstrated that excitation is conducted by the phloem of the vascular bundle, and that conduction in this tissue can be modified experimentally by the same means as is that in animal nerve. The conducted excitation may, therefore, be justly spoken of as nervous impulse and the conducting tissue as nerve.

"It has been further shown that, as in the animal, it is possible to distinguish sensory or afferent and motor or efferent impulses, and to trace the transformation of the one into the other in a reflex arc. The observations involve the conception of some kind of nerve-centre. No structure corresponding to the nerve-ganglion of an animal has, indeed, been discovered in the pulvinus of *Mimosa pudica*, but it is not impossible that the physiological facts may one day receive histological verification."

The difficulty, of course, is that neither plant physiologists nor animal physiologists are as yet inclined to accept Professor Bose's evidence quite at its face value. But the fact that the matters discussed are still under judgment, and the subject of controversy, in no wise detracts from the interest and value of this well written book, as a document of record.



KURZES LEHRBUCH DER ALLGEMEINEN BAKTERIENKUNDE.

By *Rudolf Lieske.* *Gebrüder Borntraeger*
G. M. 15 *Berlin*

6½ x 10; viii + 338 (paper)

This is a valuable and interesting contribution to the literature of general biology. As the author points out, bacteriology began as one of the special fields of botany. But as soon as it was learned that bacteria were the causes of various diseases of plants, animals, and men the practical importance of this discovery led at once to the development of highly specialized subdivisions of the science of bacteriology, which in their evolution have come at the present time to have little relation to each other. The whole subject of bacteriology is now at the threshold of what will perhaps prove ultimately to have been a radical turning point in its scientific development. New and old points of view stand at the present time in rather sharp contrast. The object of the author in writing this book was to put into the smallest space consistent with clearness and sound treatment, what a student ought to know about the general biology of bacteria before he embarks upon one of the special divisions of bacteriology such as medical, agricultural, or any other. This task, for which there was a real need, has been well done by Doctor Lieske. The topics treated are as follows: Mor-

phology; physiology; enzymes; action of external influences upon bacteria; bacterial symbioses; antagonistic relations between bacteria and higher organisms; the bacteriophage; particular biological groups of bacteria and related organisms; and technical methods of bacteriology. The book is well documented and indexed.

VERGLEICHENDE MORPHOLOGIE DER PILZE.

By *Ernst Gäumann.* *Gustav Fischer*
28 marks 6½ x 10½; x + 626 (paper) *Jena*

This systematic treatise on the morphology of the fungi by the Botanist of the Swiss Agricultural Experiment Station has as its leading idea to bring the results which have been obtained by bringing modern cytological technique to bear specifically on the taxonomy and comparative morphology of this group. The opening general part of the book contains nothing particularly new, but is an excellent summary of present knowledge of the morphology of the fungi, such as might appropriately find a place in a general text-book of botany. This is followed by a special part in which the different orders are separately discussed in detail. The book is well illustrated, thoroughly documented as to literature, and has a detailed index. Altogether it is a valuable addition to the reference literature of botany, although it is to be regretted that the treatment is so exclusively morphological.



ROOT DEVELOPMENT OF FIELD CROPS.

By *John E. Weaver.* *McGraw-Hill Book Co.*
\$3.00 6 x 9; xii + 291 *New York*

This is a detailed and rather technical treatise on a highly specialized and

neglected field of botany, the habits of the roots of plants. Attention is strictly confined to crop plants. In the different agricultural experiment stations a good deal of work has been done in this field, but it has never before been collected together. Approximately the first half of the book is devoted to general topics regarding root development, such as the soil, the morphology of roots, and the behavior of roots of numerous plants. The remainder of the book contains special chapters on different important crop plants. There is a bibliography of 232 titles, and an excellent index.



THE HYDROSTATIC SYSTEM OF TREES. *Carnegie Institution of Washington Publication No. 373.*

By D. T. MacDougal. *Carnegie Institution Washington*
\$2.50

6 $\frac{7}{8}$ x 10; iii + 125 (paper)

This is a detailed report of the more recent results of the author's extensive investigations on the hydrodynamics of the plant. The experiments here reported were performed on pine, oak, and walnut trees. Three mechanically distinct regions in the trunk are recognized as of fundamental importance in the hydrostatic system of a tree. The first of these is a complete cylindrical shell of living cells in the cambial zone, through which nothing may pass except by diffusion through protoplasm. The second shell is formed by the water column extending, under varying tensions, from the menisci of the transpiring cells in the leaves downward through the recently formed conduits and wood-cells to the root-hair zones in the roots. Finally, in the older central part of the stem, the tracheids contain air and constitute a third component of the system. All of the

results of this work are stated to confirm Dixon's conception of the cohesive meshwork column of water as the essential element in the hydrostatic system.



LEHRBUCH DER PFLANZENPHYSIOLOGIE. (*Chemische Physiologie. Band I.*)

By S. Kostytschew.

Julius Springer
Berlin

27 reichsmark

6 $\frac{1}{2}$ x 9 $\frac{3}{4}$; vii + 567 (paper)

The first article in the author's creed is that the present day worker in the field of plant physiology must be a trained chemist. In writing this book he has assumed a rather comprehensive knowledge of organic chemistry on the part of the reader. The topics discussed in this first volume are: The bases of chemical plant physiology; the assimilation of the sun's energy by green plants and the primary synthesis of organic substances; chemosynthesis and assimilation of molecular nitrogen; the nourishment of the plant with organic compounds; the nourishment of the plant with ash components and its significance; carbohydrates and proteins and their metabolism in the plant; secondary plant substances; respiration and fermentation.

The book carries rather extensive documentation of the literature and a meager and unsatisfactory index. It will be a useful and important reference book, which one would suppose will ultimately be translated into English.



AN OUTLINE OF PLANT GEOGRAPHY.

By Douglas H. Campbell. *The Macmillan Co.*
\$4.00 5 $\frac{1}{4}$ x 8 $\frac{3}{4}$; ix + 392. New York

This book is the outcome of the author's

excursions, during more than thirty years past, into many parts of the world in search of material for his botanical studies. It seems to us that the book gains both in charm and in value from the fact that Professor Campbell is not primarily a plant geographer, but has approached this field of botany with a certain spirit of detachment. After an introduction which deals primarily with the succession of plants in geological time, the book discusses the following topics in order: climatic zones; the North Temperate zone; the Palaeotropics; the Neotropical region; the South Temperate zone. The book is well illustrated, many of the photographs being original, and closes with a detailed and adequate index. It is a valuable contribution to botanical literature.



STUDIES ON THE ORIGIN OF CULTIVATED PLANTS.

By N. I. Vavilov.

Institut de Botanique Appliquée et d'Amélioration des Plantes.

— 7 x 10 $\frac{3}{8}$; 248 (paper) Leningrad

This extensive and well illustrated monograph on the origin of cultivated plants by the well-known Russian plant geneticist presents the following topics in detail: Methods of determining the geographical centers of the origin of cultivated plants; geographical centers where the forms of the principal cultivated plants of the Old World have originated; weeds as the progenitors of cultivated plants; mountain districts as the home of agriculture; the origin of primary crops, in particular of cultivated hemp; the ecological principle in the origin of cultivated plants; geographical regularities in the origin of the forms of cultivated plants; the principal world centers of the origin of cultivated plants.

KLIMA UND BODEN IN IHRER WIRKUNG AUF DAS PFLANZENLEBEN.

By Henrik Lundergardh.

Gustav Fischer

24 marks

Jena

6 $\frac{1}{2}$ x 9 $\frac{1}{2}$; viii + 419 (paper)

This is a systematic textbook of ecology, first developed as a series of lectures in the Masaryk University in Brünn. After a brief historical introduction, the following topics are discussed: The light factor; the temperature factor; the water factor; the formation and general ecological characteristics of the soil; the physical characteristics and aeration of the soil; chemical soil factors; the microorganisms of the soil; the carbon dioxide factor; the guiding principles of experimental ecological investigations. The book is well illustrated and indexed. The author takes throughout the commendable viewpoint that since ecology is a branch of physiology the attitude of physico-chemical precision which has proved so fruitful in laboratory physiology must also be the manner of approach to the problems of ecology.



GEOGRAPHIE DER MOOSE.

By Th. Herzog.

Gustav Fischer

27 marks

Jena

6 $\frac{1}{2}$ x 10; xi + 439 + 8 plates (paper)

This systematic treatise on the geographical distribution of the mosses, by the Professor of Botany at the University of Jena, is divided into three parts. The first 74 pages deal rather briefly with such general matters as the comparative anatomy of the mosses, and their technical ecological characteristics. In the two remaining parts the known facts about the geographical distribution of these plants are presented successively in two different ways. In Part II the point of departure is taxonomic. The facts about the distribu-

tion of each family, and in less detail each genus and species, are briefly set down. In the third, and final part, the point of departure is the geographic region. For each such region the moss flora is described in detail. There is a bibliography of 633 titles, and detailed indices. The book will be a valuable work of reference.

the orders and all but a few of the smaller families of Dicotyledons, with frequent illustrations of typical forms. Special emphasis is given to the British flora. There are 279 illustrations and an excellent detailed index. A glossary of technical terms would have much enhanced the value of the work to all but the professional systematic botanists.



UNTERSUCHUNGEN ÜBER DIE
BEDEUTUNG DER BAUMMY-
KORRHIZA. *Eine ökologisch-physiologische Studie.*

By Elias Melin.

Gustav Fischer

7.50 marks 6½ x 9½; vi + 152 (paper) Jena

This is a thorough review of our present knowledge of the symbiotic relation between fungi (*Mycorrhiza*) and the roots of certain trees, together with the results of the author's extensive original work on this problem. He has approached the matter experimentally and cultivated separately in pure cultures the root fungi and also the plants, and then in combination pure cultures of the plants and fungi together. It is demonstrated that the *Mycorrhizae* have a vital significance for the plants and trees on certain kinds of soil. There is an excellent bibliography covering six pages.



THE CLASSIFICATION OF FLOWER-
ING PLANTS. *Volume II. Dicotyledons.*
By Alfred B. Rendle. The Macmillan Co.

\$10.50 5¾ x 8¾; xix + 636 New York

This second volume follows the first after an interval of twenty years. It deals with the Dicotyledons. The general arrangement follows that of Engler's *Syllabus der Pflanzenfamilien*. Brief, but adequate, descriptions are given of all

THE ASPERGILLI.

By Charles Thom and Margaret B. Church.

The Williams & Wilkins Co.

\$5.00 6 x 9; ix + 272 Baltimore

A detailed, systematic treatise on the fungi of the genus *Aspergillus*. The authors have found, and base their account upon, the original descriptions of all but three of the known species of this genus. In the case of these three they were compelled to rely upon secondary references. The work has been done with great care and the book will be a valuable addition to the shelves of every biological laboratory for, as the authors truly say, the *Aspergilli* are "the weeds of the culture room."



DIE ENTWICKLUNGSLINIEN DER
KAKTEEN.

By Alwin Berger.

Gustav Fischer

6 marks 6¾ x 10; iv + 105 (paper) Jena

A detailed, technical study of the phylogeny of the cacti. The book is abundantly illustrated with superb photographs beautifully reproduced. The author is of the opinion that the oldest cacti were tropical plants, and that early in their migration from the south into America they split into three main stem lines from which the present forms developed.

MORPHOLOGY

ÉTUDE MORPHOLOGIQUE ET MORPHOGÉNIQUE DU SQUELETTE DU BRAS ET DE L'AVANT-BRAS CHEZ LES PRIMATES. *Archives de Morphologie Générale et Expérimentale. Fascicule 24.*

By Ioan Gh. Botez. Gaston Doin et Cie
30 francs 6½ x 10; 174 (paper) Paris

This interesting monograph deals with the anatomy and development of the bones of the arm in the primates. Its point of view is that of modern physiological morphology. In particular, the author develops his evidence to show that, from the morphogenetic point of view, bone is not strictly a passive element fashioned by muscle as the active element, but on the contrary bone and muscle transform themselves simultaneously in their development in a relation of reciprocal dependence, in integration with the general state of organic equilibrium of the individual. There is a bibliography of 171 titles.



LA TÊTE. *Essai d'Anatomie Synthétique. Anatomie Médico-Chirurgicale. Anatomie des Formes Extérieures et Anatomie des Régions. Fascicule I. Le Crane. Fascicule II. La Face.*

By Philippe Bellocq. Masson et Cie
25 francs (2 volumes) Paris
8½ x 11; 260 (paper)

These volumes are based on the author's lectures in anatomy at Strasbourg, collected by Dr. Alfred Weiss, and edited and put in order for publication by Professor Bellocq. The first volume deals in detail with the anatomy of the skull and the meninges. It is illustrated with 36 figures, nearly all original and in the form of semi-diagrammatic line cuts. The second volume treats in the same way the anatomy of the face, with 46 illustrations.

The volumes constitute a sound contribution to purely descriptive human anatomy.



PHYSIOLOGY

PRINCIPLES OF HUMAN PHYSIOLOGY.

By Ernest H. Starling. Lea and Febiger
\$8.50 6¼ x 9¾; xiii + 1074 Philadelphia

There are extremely few men living today who could by any possibility give an adequate picture of the existing status of any large branch of science. Professor Starling modestly denies his ability to do this for physiology and graciously acknowledges aid from a number of his colleagues in the preparation of this fourth edition of his masterly textbook. But after making all due allowance for this help the reader cannot but stand aghast at Professor Starling's extraordinary genius for critically envisaging an enormous field of human knowledge. In conformity with a tendency manifest in a number of recent general physiological works, the amount of space devoted to biochemical matters has been reduced in this edition, which recognizes the development of a considerable degree of autonomy of this branch. The book will long continue to rank as one of the great standard reference works.



TROUBLES DES ÉCHANGES NUTRITIFS. *Physiologie, Pathologie, Thérapeutique. Tome I et II.*

By Ch. Achard. Masson et Cie
110 francs (2 volumes) Paris
6½ x 10; vi + 1220 (paper)

One cannot but admire the courage of a man who, in this day of rapid advance in biochemical knowledge, attempts unaided to write a 1220 page textbook on the

diseases of metabolism. The project was begun in 1912, was interrupted by the war, and has only now been brought to completion. Unfortunately, as Achard foresaw, no one man can cover such a large field, and even if he could, it would be impossible to get such a big book through the press in time to have it up to date. Furthermore, anyone, and perhaps particularly a Frenchman, is inclined to make such a work provincial by basing his views almost entirely upon the contributions of his own countrymen. Achard's book will serve as a mine of information for anyone who wants an *entrée* into the French literature on metabolism, but it will hardly satisfy an American who will find in it so little mention of what is commonplace on this side of the water. Even such a well known procedure as the phenolsulphonephthalein kidney function test is mentioned only in a short footnote; the blood and bile pigments are discussed without reference to the work of Whipple and his students, and Ambard's quotient is treated at length without reference to the extensive and careful work of Addis. There is a good index.



HANDBUCH DER PHYSIOLOGIE
DER NIEDEREN SINNE. (*I. Band: Die
Physiologie des Geruchs- und Geschmacks-
sinnes.*)

By Emil von Skramlik.

Georg Thieme

31.50 marks

Leipzig

6 $\frac{3}{4}$ x 10 $\frac{1}{4}$; viii + 532 (paper)

There has long been needed a comprehensive and critical review of the present state of knowledge of the physiology of the so-called lower senses (in contrast to sight and hearing). Zwaardemaker's valuable book on smell dates as far back as 1895. Doctor Skramlik, who is associate professor of physiology at Frei-

burg, proposes to fill this gap in the literature with the present treatise. This first volume deals with the senses of smell and taste. Two succeeding volumes will cover the senses of pressure (touch), heat, cold and pain. The volume before us is well done, carrying a sufficient amount of detail in the treatment, and yet achieving some degree of synthetic unity. Detailed references are given to the extensive literature. The book is well illustrated and thoroughly indexed.

HUMAN PHYSIOLOGY.

By John Thornton. Completely revised by
William A. M. Smart.

Longmans, Green and Co.

\$3.75 5 $\frac{1}{2}$ x 8 $\frac{1}{2}$; vii + 463 New York

This third edition of a well-known quiz compend of human physiology has been thoroughly revised and in considerable part rewritten. By reason of its moderate size and the clear-cut manner of presentation it is not a bad resource for the general reader who wishes to get, without too much trouble, a reasonably comprehensive review of the present state of knowledge regarding human physiology. At the end there is a list of examination questions, partly original and partly selected from papers set in London examinations, followed by a glossary of technical terms and a detailed index. The book is extensively illustrated, mainly with borrowed cuts.



PHYSIOLOGICAL PAPERS. *Dedicated
to Professor August Krogh.*

Wm. Heinemann (Medical Books) Ltd.

30 shillings

London

7 $\frac{1}{2}$ x 10 $\frac{1}{2}$; xvi + 375 (paper)

This *Festschrift* to the distinguished Danish physiologist contains twenty-two papers by Professor Krogh's former

students and associates, dealing with a wide range of physiological problems. The occasion which called forth the volume is a dual one; Professor Krogh's fiftieth birthday, and the removal from the old laboratory in Ny Vestergade to the new building erected for Professor Krogh's work through the munificence of the Rockefeller Foundation. The volume is beautifully printed and illustrated, with a fine portrait of Professor Krogh as frontispiece.



FOIE, PANCRÉAS, RATE.

By Dr. Mathieu de Fossey. G. Doin et Cie
10 francs $4\frac{3}{4} \times 6\frac{1}{8}$; 164 (paper) Paris

A quiz compend on the diseases of the liver, pancreas, and spleen, with especial reference to methods of treatment and therapeutics.

BIOCHEMISTRY

DAS KOLLOIDE GOLD. (*Kolloidforschung in Einzeldarstellungen. Herausgegeben von R. Zsigmondy. Band 1.*)

By R. Zsigmondy and P. A. Thiessen.

Akademische Verlagsgesellschaft M. B. H.
Marks 7 $6 \times 8\frac{3}{4}$; x + 229 (paper) Leipzig

DAS KOLLOIDE GOLD IN BIOLOGIE UND MEDIZIN. *Die Goldsolreaktion im Liquor Cerebrospinalis. (Kolloidforschung in Einzeldarstellungen. Herausgegeben von R. Zsigmondy. Band 2.)*

By Ernst Joël.

Akademische Verlagsgesellschaft M. B. H.
6 marks $6 \times 8\frac{3}{4}$; 115 (paper) Leipzig

These first two volumes in a new series under the general editorship of Professor Zsigmondy, are primarily of technical interest to the student of colloid chemistry, and to physiologists and clinicians interested in the application of the

colloidal gold technique to diagnostic and similar biochemical reactions.



LEITFADEN DER KOLLOIDCHEMIE FÜR BIOLOGEN UND MEDIZINER.

Eine Einführung in die Allgemeine Physiologie, Pathologie, Pharmakologie.

By Dr. Hans Handovsky. Theodor Steinkopff
12 marks Dresden

$6\frac{1}{4} \times 9\frac{1}{4}$; xvi + 265 (paper)

The second edition of an introductory text-book of colloid chemistry, written especially from the point of view of the interests of biologists and medical men. It opens with a discussion of the general characteristics of disperse systems and the origin of such systems, followed by an account of the mechanical and electrical properties of disperse systems in general, and particularly colloid disperse systems. The last two sections of the book deal with the reactions of colloid systems and the structure and properties of gels. In an appendix there is discussed in an interesting general way the application of colloid chemistry to biological problems.

PROTEINS. *Lectures given in the United States of America in 1924.*

By S. P. L. Sørensen.

The Fleischmann Laboratories

$6\frac{1}{4} \times 9\frac{1}{4}$; xx + 142. New York

This volume published by The Fleischmann Laboratories as a souvenir of the recent visit of Professor Sørensen to this country is useful, because it presents in convenient form the author's latest results and views regarding the chemistry of proteins. Besides the purely technical articles on proteins, there is an interesting chapter on the chemistry of bread making, with especial reference to the influence of hydrogen ion concentration. Unfortunately the book is not indexed.

SEX

Vacant

BIOMETRY

ZUWACHSRÜCKGANG UND WUCHS-STOCKUNGEN DER FICHTE IN DEN MITTLEREN UND UNTEREN HÖHENLAGEN DER SÄCHSISCHEN STAATSFORSTEN.

By *Eilhard Wiedemann.* *Walter Laux*

6 $\frac{1}{2}$ x 9 $\frac{3}{4}$; 190 (paper) *Tharandt, Germany*

This is a detailed biometric and general ecological investigation to determine the causes which are leading to the general damping off of the growth curve of the trees in the pine forests of Saxony. The broad conclusion is that the supposed laws of forest production do not have general validity, but the local situation must be taken into account in all cases because some peculiarity in it may markedly alter the growth curves. There is a bibliography of 169 titles. The study will be found of interest by ecologists as well as professional foresters.



PSYCHOLOGY AND BEHAVIOR

OUTLINE OF ABNORMAL PSYCHOLOGY.

By *William McDougall.*

Charles Scribner's Sons

\$4.00 6 x 8 $\frac{3}{4}$; xvi + 572 *New York*

The author states that this volume is really to be considered as the second part of his well-known "Outline of Psychology." The two books taken together thus form a comprehensive treatise on the science of the mind in both its normal and pathological aspects. Professor McDougall's competence to deal with abnormal psychology is unusual, for he has had not only the purely scientific

training and experience of the academic psychologist but also a medical training and extensive experience with clinical aspects of mental disorders. The result is a sounder and saner account than is to be found in much of the psychiatric writing of the present day. The general biologist, and particularly the student of animal behavior, will find the book especially useful in giving him a critical review of a field of study which is at once somewhat remote and recondite, but at the same time important to his own work.



TIERPSYCHOLOGIE. *Vom Standpunkte des Biologen.*

By *Dr. Friedrich Hempelmann.*

Akademische Verlagsgesellschaft M. B. H.

M. 32 *Leipzig*

6 $\frac{1}{2}$ x 9 $\frac{3}{4}$; viii + 676 (paper)

This is a thorough, critical and synthetic review of the literature of animal behavior. Somewhat more than half of the book—the special part—deals with the material on a taxonomic base, starting with protozoa and ending with vertebrates. The remainder of the book—the general part—discusses such general points as sensation, the brain as the organ of mind, the history and methodology of animal psychology, etc. There is an extensive bibliography covering 26 pages set in small type. The book is somewhat too sparsely illustrated, but contains excellent detailed indices. Altogether it is a treatise which every student of any aspect of animal behavior must have in his library.



LE DRESSAGE DU CHIEN DE CIRQUE.

By *J. Dbers.* "*Les Éditions de l'Éleveur*"

12 francs 4 $\frac{1}{2}$ x 7 $\frac{1}{2}$; 85 (paper) *Paris*

This little treatise on the training of dogs for the circus and vaudeville stage,

by an "artist of the circus," will be found not only entertaining but of real and significant interest by the student of animal behavior and comparative psychology. It is a thoroughly practical treatise, written with characteristic French objectivity and precision. Everyone will be glad to know that the author's system of training grounds itself upon kindness, patience and understanding of the psychology of the dog, rather than upon fear, punishment, and cruelty. We commend the book highly to biologists, as well as to the trouper.



DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

NATURE'S ALCHEMY. *Special Bulletin of the Turck Foundation for Biological Research, etc.*

The Turck Foundation for Biological Research
— 8½ x 11; 62 New York

This entertaining volume tells all about Dr. Fenton B. Turck, The Turck Foundation for Biological Research, cytost, and anti-cytost. It was prepared under the supervising editorship of Mr. Hamlin Garland, 507 Cathedral Parkway, New York City, from whom biologists can probably obtain free copies. The following quotations will perhaps indicate the desirability of so doing:

"That cells cannot automatically perform the functions of growth, that they must be stimulated to action, is established. That each cell holds within itself a 'self-starter' is also agreed upon. This substance has been variously named 'cell-sap,' 'tissue extract,' and the like. LaMarck (*sic*) called it 'that subtle fluid,' but Turck named it 'cytost' from the Greek word *cytos*, meaning cell.

"For more than thirty years Turck has been experimenting with this 'activating principle,' one of the most powerful

and mysterious elements in nature, and it is upon the character and action of 'cytost' that his activities are still concentrated.

" From a long series of experiments in his laboratory he demonstrated that many disorders in animal tissue were due to abnormal cell breakdown and the liberation of excessive quantities of cytost into the cell media. Just as excess of cytost in the soil is the cause of disease in plant tissue, so excess of animal cytost in the fluids surrounding the cell produces disease and death in animals.

"He demonstrated as many others from LaMarck (*sic*) to Conklin had done, that the cell contained its own activating element, but he went further. 'No matter what the agent which liberates this element may be,' he says, 'we have shown that in certain measured concentrations cytost stimulates the growth of tissue, in larger amounts it destroys tissue.'

"Absolutely necessary to the cell in dilute proportions, it is in excess injurious to the cell. Like electricity, it is stimulating when acting as a light charge, but acts as a disrupting force in case of high power.

"Turck demonstrated other and still more marvellous properties in this element. He found by actual experiment that it was *specific to the species*, that is to say, cytost obtained from the tissues of a cat's heart was different in quality and action from cytost extracted from the tissues of a dog's heart. In the one case the cytost carries a charge of 'cat' and in the other a charge of 'dog.'

"From a study of the varying degrees of resistance to the action of cytost on the part of different animals, it was but a short step to the production of immunity. Reasoning that there must be a counterbalancing element in the blood of the immunized animal, Turck carried out experiments which not only raised the

animal's resistance to disease to a very high degree but led to the isolation of the opposing element.

"Injecting cytost made from human tissue into a horse at intervals over several months' time, he demonstrated that the animal had built up in its blood a substance which strongly tended to offset the toxin action of the cytost, for when a portion of the animal's blood was drawn, dried and *burnt to an ash* there remained in the mineral salts of this ash, an element which proved to be the *negative* charge as cytost was the *positive* charge of the life force.

"This counter-balancing substance which he thus isolated and used in creating a higher degree of resistance to disease in the human organism he very naturally named Anti-cytost.

"Having in his possession and under his control both of these subtle elements, he was able to produce in this laboratory by their use in action and re-action, both active and passive immunity in animals. After hundreds of experiments with these opposing substances he came to the momentous conclusion that *health is a dynamic or continuing equilibrium between them* and that the cell is the meeting point of two all-pervasive life forces, a minute stage on which these positive and negative powers strive for the mastery.

"The man of science cannot use the word 'marvellous' but we as laymen permit ourselves to wonder at the patience and skill with which Turck has brought his conception to a concrete demonstration.

"In many of his experiments, Turck has found the germ a 'secondary invader.' Germs of one kind or another are always present in the organism but appear to have no potency until a break in the tissue occurs.

"In the *Medical Record*, May, 1919,

Turck makes report of various experiments in which he sprayed into the nostrils and throats of cats, varying quantities of pneumonia organisms, causing no pneumonia, but when he mixed cytost with these germs, pneumonia at once developed. He produced pneumonia at will by the use of lung-tissue autolyzed under sterile conditions. By spraying, by injection and by covering the paws of animals with a paste of lung-tissue he obtained typical pneumonitis.

"Another and equally significant experiment involved the gathering and burning of the dust of the room in which cytost had been produced and in which various demonstrations had taken place. Upon reducing this dust to an ash, and adding a portion of sterile water, Turck obtained sufficient cytost to kill a cat.

"This experiment with the dust of the room burned to an ash, suggests that the over-crowding which leads to disease in tenements, is not solely a question of germ infection, but also of the presence of cast-off cell debris.

"There are still wider reaches to Turck's experimentation. Extending his interest to the parent cell, he proceeded to demonstrate that the size, weight, vitality and fecundity of animals could be affected by the graduated use of cytost.

"Taking flocks of fowls, litters of kittens and rabbits, he separated them into groups, some to be held as normal 'controls' while the others were being treated by injection of cytost. The treated animals outgrew their fellows, were more active, lived longer, and were more fecund.

"Furthermore, he found that he could not only build a larger and finer animal organism by the use of cytost, but that the increased hardihood, the larger size, the finer fur, and other individual excellencies of the parents were transmitted to the offspring. He was able not only to

stimulate the growth of guinea pigs and cats, but to lengthen the life of succeeding generations. Laboratory animals of the third and fourth generation continue to show the benefits transmitted to them.

"The results of these experiments have been tabulated and published in various medical and surgical journals. His protocols show that the laying power of hens has been increased by the use of this natural cell stimulant, and that the fur of cats and guinea pigs was made richer and glossier, all evidences of increased vitality."

In spite of the prohibition quoted above we think that every man of science will yield to the overwhelming temptation and say MARVELLOUS!

HAVELOCK ELLIS. *A Biographical and Critical Survey.*

By Isaac Goldberg Simon and Schuster
\$4.00 5 $\frac{3}{4}$ x 8 $\frac{1}{2}$; xiv + 359 New York

The author has not succeeded so well in the application of his somewhat novel biographical technique to Havelock Ellis as he did in his first essay in that direction, with H. L. Mencken as the subject. After finishing the volume the reader is still not satisfied that he knows very much

about the real Havelock Ellis. There is a great deal in the book about Mrs. Ellis and her writings. The emphasis throughout is on the literary side of Ellis' character and work. What makes the volume particularly disappointing to the biologist is the inadequacy of the discussion of his scientific work. However, it must be said that the book taken as a whole gives a more informing picture of a great contemporary than anything else now available. It is less extensively and less significantly illustrated than was the Mencken volume.

ENSEIGNEMENTS NATURELISTES

By Dr. Paul Carton Norbert Maloine
15 francs 4 $\frac{3}{4}$ x 7 $\frac{1}{2}$; 384 (paper) Paris

A fine piece of quackery proving conclusively that, even with Abrams to our credit, we have no monopoly of the breed in this country. A "naturalist" is a person who is against good food, good drink, good tobacco, and most of the other achievements of pleasant living. Raw vegetable foods are the key to health, wealth, and happiness. Those who find enjoyment in the contemplation of the manifestations of the outlying aberrations of the human intellect will be entertained by this volume.



THE COST OF BIOLOGICAL BOOKS IN 1926

BY RAYMOND PEARL

During the first year of the existence of THE QUARTERLY REVIEW OF BIOLOGY there have been noticed in the department devoted to *New Biological Books* somewhere in the neighborhood of 300 separate books. I have been interested to note the considerable variation in their prices, as they have come in to the editorial office. This has led me to prepare a brief summary of the situation as it has developed during the year 1926. It is proposed to make such a *résumé* of the book price situation an annual feature.

I have first of all classified the books which have been reviewed in our pages according to the country of publication, under the following rubrics:

I. *The United States*. Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of the books reviewed during the year have had this origin.

II. *Germany*. In the number of books sent in by publishers for review Germany stands next to this country. There has grown during the year a strong feeling in the editorial office that German publishers of scientific books, as a class, are distinctly more wide-awake and enterprising in their attempts to secure a world-wide distribution of their product than are the corresponding groups in other European countries.

III. *English-American*. In this group are placed the books which are manufactured and published in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England*. In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France*. This group includes all books published in France and her colonies.

VI. *Other Countries*. Here are placed all books published in any other country than those specified above.

VII. *United States Government*. In any discussion of book prices it would be manifestly unfair to include government publications with the product of American commercial publishers.

In the table which follows there are given, for each of the sources of origin listed above, the following items:

a. Total number of pages in the books which have been reviewed in Volume I of THE QUARTERLY REVIEW OF BIOLOGY, *excluding* those books which either had no price, because they were intended for free distribution, or because we were unable to find out, after diligent inquiry, what the price was. Anyone who has had no experience of the matter would be amazed at the number of books which are distributed by their publishers without any indication whatever, on either book or wrapper, as to what it is proposed to charge for them. Not infrequently it takes two or more letters to extract this information from a reluctant publisher. Just why they are so set on keeping the matter secret is impossible to say.

b. The total cost, in dollars, of those books having their total pages given in the first column. In computing these values for books originally priced in a foreign currency I have used the exchange

rates prevailing at the time the book was received. These prices then represent fairly what an American biologist would have had to pay if he had bought these books at the time they came to us.

c. By the simple process of dividing the figures in the second, or *b* column, by those in the first, or *a* column, we arrive at those in the last column, which therefore give the average *price per page* of the aggregate of books received from the several sources. By judicious attention to the location of the decimal points these prices in the last column of the table are exhibited as so many *cents per page*.

Prices of Biological Books, 1926

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			<i>cents</i>
English-American.....	7,938	\$122.65	1.55
Other countries.....	1,799	27.13	1.51
England.....	5,423	69.48	1.28
United States.....	43,049	480.87	1.12
Germany.....	16,431	179.23	1.09
France.....	5,306	18.42	0.35
U. S. Government.....	2,629	8.25	0.31

On the basis of cents per page it appears from the table that the books emanating from the American branches of English publishing houses have been the most expensive during the past year, so far at least as may be judged from these samples. The next most expensive, as a class, are those published in the "Other Countries" not separately specified. Then follow the English books, and then those published in the United States. At about the same level, but actually 0.03 of a cent lower per page, come the German books. The only cheaper class of commercially published books are the French, which have had the lowest price of all such, costing only slightly more per page than the United States Government publications.

In interpreting these results certain outstanding factors need to be kept in mind. In the first place the English-American have had to pay duty to enter the United States, and the prices here quoted for these books include the duty. There is presented here to the American biologist a concrete illustration of the meaning to him of protecting infant industries. There are those who have contended, and spent much of their personal time and energy in a vain endeavor to convince our legislators, that the taxation of intellectual progress was neither good business nor exactly sporting. But some of the American publishers and about all the printers think otherwise, and they speak a language more easily understood by our lawgivers.

In the case of books listed under the heads "England" and "Other countries" (so far as the latter are in the English language) the prices do *not* include duty. But the American biologist would have to pay duty, and therefore the price to him would be even higher than the table shows.

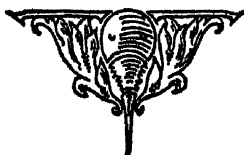
There is a widely prevailing impression that the German publishers are greatly over-pricing their products at the present time. This does not seem to be the case, so far as the present sample of new biological books is concerned. Making due allowance for the fact that the majority of the German prices included in the table are for books in paper covers, it turns out that the biological books received from Germany during 1926 cost almost exactly the same per page as those turned out by American publishers. And any American publisher can prove that he is selling his books at just as low a price as he can afford to and escape bankruptcy proceedings. Perhaps German books ought to sell lower than those published here, because of generally lower labor costs in Germany,

but there are other complicating economic factors which enter the case.

Of all places in the world during 1926 France has been the spot of choice to buy books. French publishers have signally failed to adjust their prices correctly to the degree of emaciation of the franc. What will happen in the future a mere biologist cannot predict. But there is a possibility, at least, that presently the French publishers will over-compensate

in this matter, as the Germans are alleged to have done when their currency became stabilized, and put their prices as much too high as they have been too low in 1926.

Finally there must be a word of appreciation of the boon which the Government Printing Office is to American scientific men. It regularly publishes memoirs of the first importance and distributes them at a price which makes them available to even a beginning instructor.



INDEX

- Abraxas*, gynandromorphism, 328
 Achard, Ch., Diseases of Metabolism, 599
 Adaptation, horse, 171
 mammals, 175
 Age and area, 212
 Age and area, 553
 barriers, 563
 constant conditions, 555
 development, 554
 group of allied species, 560
 list of literature, 571
 recent literature, 564
 size and space, 555
 swamping and dying out, 569
 Aggressivity, parasitism, 407
 Alcohol, effects on testis, 31
 Allee, W. C., and Allee, M. H., Jungle Island, 586
Amblystoma, nervous system, 63
 Ameba, behavior, 115
 chromatin, 107
 chromidia, 110
 contractile vacuoles, 105
 cytoplasmic differentiation, 96
 cytoplasmic division, 107
 ectoplasmic ridges, 103
 endoplasmic crystals, 104
 flagellate stage, 111
 genetics, 111
 "hair", 102
 metaplastic grains, 105
 mitosis, 109
 movement, 112
 nucleus, 106
 plasma membrane, 98
 pseudopods, 98
 regeneration, 111
 Amoebae, man, 394
Anchirbertium, 166
 Animals in lakes, 572
 Anthropology, 360, 465
 Apes, fetuses, 467
 Aquatic vegetation, 573
Archaeobippus, 166
 Artschwager, E., Botanical Dictionary, 130
Ascaris megalocephala, 420, 421
 Ass, 147
 Baboon, fetal growth, 477
 Baker, S., Portraits in the London Zoo, 454
 Barnard, J. E., and Welch, F. V., Practical Photomicrography, 450
 Baumgartner, W. J., Fetal Pig, 307
 Bayliss, Sir W. M., Enzyme Action, 134
 BEAN, R. BENNETT, Human Types, 360-392
 Beebe, W., The Arcturus Adventure, 590
 Jungle Days, 130
 Behavior, ameba, 115
 plants, 236
 Bellocq, P., Anatomy of the Skull, Meninges and Face, 599
 Berger, A., Phylogeny of the Cacti, 598
 Bergey, D. H., Determinative Bacteriology, 306
 Berkeley, W. N., Endocrine Medicine, 459
 Bertin, L., and Boisselier, A., Laboratory Manual in Zoology, 594
 Bigelow, H. B., and Welsh, W. W., Fishes of Maine, 129
 Bigelow, R. P., Dissection of the Cat, 307
 BIOCHEMISTRY (book reviews), 133, 308, 460, 601
 BIOLOGY, GENERAL (book reviews), 125, 299, 448, 585
 HUMAN (book reviews), 127, 301, 450, 587
 BIOMETRY (book reviews), 135, 309, 462, 602
 Birds, gynandromorphism, 329
 Birkner, F., Prehistoric Man in Central Europe, 590
 Blanchard, F. N., Key to Snakes, 454
 Blunck, H., Insect Biology, 300
Bombinator, nervous system, 62
 Bonar, L., Holman, R. M., and Roush, L., General Botany, 306
 Bose, J. C., The Nervous Mechanism of Plants, 594
 BOTANY (book reviews), 130, 305, 455, 594
 Botez, I. Gh., Anatomy and Development of the Bones of the Arm in Primates, 599
 Boubier, M., History of Ornithology, 454
 Browning, W., Medical Heredity, 302
 Buchanan, B. E., Bacteriology, 130
 Bush, A. D., College Text-book of Physiology, 459
 Calkins, G. N., Biology of the Protozoa, 451
 Calmette, A., Tuberculosis, 127
 Campbell, D. H., Plant Geography, 596
 Cannon, W. A., Physiological Features of Roots, 455
Carex, 228
 CAROTHERS, E. ELEANOR, Segregation of Homologous Chromosomes, 419-435
 Carpenter, T. M., Human Metabolism with Enemata of Alcohol, 458
 Carriers, parasites, 408
 Carton, P., Instructions for "Naturists," 605
 Casserly, G., Dwellers in the Jungle, 462
 Castle, W. E., Genetics and Eugenics, 125
 Heredity in Rabbits and Guinea-pigs, 298

- Castration, 35
 Cephalic index, 502
 Chemotherapy, parasitism, 410
 Chromosomes, *Coprinus*, 201
 Crepis, 190
 Drosophila, 190
 dyads, 431
 Ectocarpus, 202
 Elodea, 195
 gens, in y-chromosome, 205
 genetics, 186
 heteromorphic, 429
 morphological differences, 422
 multiple groups, 186
 new numbers by hybridizing, 193
 Nicotiana, 195
 Oenothera, 287
 Papaver, 194
 physiological differences, 422
 Phytolacca, 208
 Primula, 195
 qualitative differences, 423
 quantitative differences, 423
 reduction, 421
 segregation of homologous, 419
 sex, 316, 433
 sex, in flowering plants, 195
 Sphaerocarpus, 198
 synapsis, 425
 Tabacum, 195
 Trifolium, 188
Circotettix verruculatus, 431
 CLEVELAND, L. R., Symbiosis between Termites and their Intestinal Protozoa, 51-60
 Cole, S. M., Physiological Chemistry, 134
 Cooper, E. R. A., Histology of Human Endocrine Organs, 457
 Craigie, E. H., Anatomy Nervous System, 131
 CREW, F. A. E., Sexuality in Animals, 315-359
 Crum, W. L., and Patton, A. C., Economic Statistics, 135
 Cryptorchidism, 6
 Cuénot, L., Adaptation, 119
 Curtis, W. C., and Guthrie, M. J., General Zoology, 305

 Daniel, R. J., Animal Life in the Sea, 453
 Darwin, L., Eugenic Reform, 587
 Davidson, J., British Aphides, 130
 De Omnibus Rebus et Quibusdam Aliis (book reviews), 310, 462, 603.
 DEWILDER, S. R., Morphogenesis in the Nervous System, 61-86
 Dewar, D., Indian Bird Life, 445
 Diers, J., Training of Dogs for the Circus, 602
 Dingler, M., Insect Pests of the Household, 593
 Dorland, W. A. N., American Medical Dictionary, 464
 Dorsey, G. A., Behavior of Human Beings, 309
Drosophila, chromosomes, 316
 gynandromorphism, 321
 intersexuality, 330
 Dublin, L. I., Population Problems in the United States and Canada, 589
 Dublin, L. I., Kopf, E. W., and Van Buren, G. H., Cancer, 303
 Dubreuil-Chambardel, L., Variations of the Human Body, 589
 Dunham, F. L., Social Medicine, 127
 Dunlap, K., Social Psychology, 137

 Eldridge, S., Organization of Life, 126
Endamoeba histolytica, 396, 402, 404, 408
 Endemics, plants, 238
Eobippus, 152
 Epidemiology, human protozoa, 395
Epibippus, 154
 Equidae, divergent lines, 164
Equus, 164
 Erskine, Mrs. M., Sex Control, 136
 Estabrook, A. H., and McDougle, I. W., Mongrel Virginians, 588
 Evans, C. L., Recent Advances in Physiology, 458
 EVOLUTION (book reviews), 124, 294, 444, 584
 horse, 139
 Eye, transplantation, 80

 Fauré-Fremiet, E., Physics and Chemistry of Growth and Development, 449
 Fenton, C. L., and Fenton, M. A., Devonian Fossils, 447
 FERNALD, M. L., Antiquity and Dispersal of Vascular Plants, 212-245
 Fetuses, age and rate of growth, 472
 apes and monkeys, 467
 asymmetries, 512
 chest, 477, 482
 face, 503
 fingers, 492
 fluctuations in rate, 473
 growth, 465
 hand and foot, 492
 head, 500
 heel, 498
 hip, 478
 human races, 466
 limbs, 486, 499
 measurements, 469
 nipples, 481
 nose, 504

- Fetuses, shoulder, 484
 species differences and rate, 475
 thumb, 493
 toes, 495
 umbilicus, 481
 variability, 507
- Fisher, R. A., Statistical Methods, 309
- Flagellates, intestinal, 51
 man, 395
- Fossey, M. de, Diseases of the Liver, Pancreas and Spleen, 601
- Fox, C., Insects and Disease of Man, 130
- Frazer, J. G., Worship of Nature, 588
- Fruwirth, C., Genetics of the Potato, 298
- Fungi and termites, 53
- Funk, C., Microchemical Analysis, 308
- Fürth, O., Physiological and Pathological Chemistry, 460
- Gager, C. S., Science and Theology, 447
- Gates, G., and Gates, A. W., Mechanism and Meaning of Life, 584
- Gäumann, E., Morphology of Fungi, 595
- Gene, for intersexuality, 334
 Y-chromosome, 205
- Genetics, amoeba, 111
 (book reviews), 125, 297, 447
 chromosomes, 186
Oenothera, 283
- Genotype, composition, 334
 distribution, 321
- GEROULD, JOHN H., Cuénot on Adaptation, 119-123
- Giardia lamblia*, 401
- Gibbon, fetal growth, 477
- Gilbert, H. A., and Brook, A., Secrets of the Eagle, 453
- Goldberg, I., Havelock Ellis, 605
- Goodrich, E. S., Living Organisms, 124
- Gowen, J. W., Cattle Breeding, 125
- Gras, N. S. B., History of Agriculture in Europe and America, 590
- Gregory, W. K., Human Dentition, 124
- Grimpe, G., and Wagler, E., Fauna of the North Sea and the Baltic, 591
- Gruber, M. von, Hygiene of Sex, 461
- Gruenberg, B., Biology, 127
- Growth, fetal, 465
 plants, 87
- Gunn, H., Empire Big Game, 592
- Gynandromorphism, *Abraxas*, 328
 bee, 324
 birds, 329
Drosophila, 321
 invertebrates, 329
 silkworm, 327
- Haberling, W., Biography of Johannes Müller, 587
- Haigh, E., Religion and Natural Science, 463
- Haim, A., Bacteriolysis, 131
- Hammond, J., Reproduction in the Rabbit, 307
- Hampton, F. A., Scent of Flowers and Leaves, 455
- Handovsky, H., Colloid Chemistry, 601
- Hannesson, G., Anthropology of Iceland, 589
- Haploids, sex, 198
- Hargitt, C. W., and Hargitt, G. T., General Biology, 301
- HÄGNER, R. W., Host-parasite Relationships, 393-418
- Helmholtz, H. von, Physiological Optics, 457
- Hempelmann, F., Animal Behavior, 602
- HENDERSON, L. J., Whitehead on Science and the Modern World, 289-294
- d'Herelle, F., Bacteriophage, 587
- Immunity, 127
- Hering, M., Biology of Butterflies, 452
- Herrick, G. W., Injurious Insects, 304
- Herter, K., Animal Behavior, 462
- Herzog, Th., Geographical Distribution of Mosses, 597
- Hibernation, 274
- Hieracium*, 558
- Hill, A. V., Muscular Activity, 307
- Hill, L., and Campbell, A., Health and Environment, 133
- Hipparion*, 164
- Hippidium*, 165
- Hirsch-Schweigger, E., Zoological Dictionary, 592
- Hitchcock, A. S., Systematic Botany, 305
- Hoffman, F. L., Homicide Problem, 301
- Hogben, L. T., Comparative Physiology, 449
- Hornaday, W. T., Wild-animal Round-up, 452
 adaptation to environment, 171
 evolution, 139
 fossil, 148
 living species, 146
- Horse, skeleton, 142
 tertiary ancestors, 150
- Host-parasite relationships, protozoa, 393
- Host-parasite specificity, 412
- Hrdlička, A., Old Americans, 301
- Human types, 360
 cerebral, 386
 digestive, 386
 muscular, 385
 physiological, 385
 respiratory, 386
- Hunt, H. R., Anatomy of the Rat, 306
- Hurst, C. C., Genetics, 297
- Hutchinson, J., Families of Dicotyledons, 455
- Hutton, S. K., Health and Disease among Eskimos, 302

- Hybridization, *Oenothera*, 283
 Hybridization and chromosome number, 193
 Hypermorph, 361
Hypobippus, 166
 Hypomorph, 361
- Immunology, parasitism, 406
 Infection, human protozoa, 397
 malaria, 164
 trypanosome, 246
 Infusoria, man, 395
 Insects, freezing and survival, 270
 Internal secretion of testis, 34
 Intersexuality, animals, 321
 Drosophila, 330
 Lymantria, 336
 mammals, 345
 Interstitial cells of testis, 6, 37
Isospora hominis, 397
- Jacobshagen, E., Comparative Morphology, 132
 Jennings, H. S., Biology and Man, 124
 Jickeli, C. F., Pathogenesis, 585
 Joël, E., Colloid Gold, 601
 Just, G., Genetics, 448
- Kalotermitidae, 542
 Kary, H. H., Evolution, 297
 KELLERMAN, K. F., Photoperiodism, 87-94
 Kendall, E. C., Thyroid Gland, 308
 Kepner, W. A., Teleology in Animal Behavior, 137
 King, J. T., Basal Metabolism, 459
 Kingsley, J. S., Vertebrate Skeleton, 131
 KLUGE, A. BROOKER, Productivity of Lakes, 572-577
 Klyce, S., Sins of Science, 310-312
 Kollmann, M., and Papin, L., Nasal Fossae of Lemuridae, 132
 Kostytschew, S., Plant Physiology, 596
 Kruif, P. de, Microbe Hunters, 313
 Kyle, H. M., Biology of Fishes, 304
- Lakes, productivity, 572
 Langdon-Davies, J., New Age of Faith, 303
 Latency, parasitism, 409
 Leathes, J. B., and Raper, H. S., Fats, 133
 Lebedinsky, N. G., Metamerism, 301
 Lehmann, E., Genetics, in *Epilobium*, 299
Leishmania, 406
 Leupold, E., Experimental Morphology, 126
 Lieske, R., General Bacteriology, 595
 Light, ecological factor, 89
 physiological significance, 91
 vegetative response, 90
 Limbs, transplantation, 61
 Lipschutz, A., Internal Secretions of Sex Glands, 135
- Locy, W. A., Growth of Biology, 300
 Loeb, J., Regeneration, 126
 Love, A. G., Medical Statistics of U. S. Army, 451
 Luckiesch, M., and Pacini, A. J., Light and Health, 308
 Lull, R. S., Ways of Life, 124
 Lundergardh, H., Plant Ecology, 597
- MacDougal, D. T., Hydrostatic System of Trees, 596
 Machin, A., Evolution of Man, 295
 Mainzer, F., Clinical Diagnosis, 314
 Malaria, bird, 164
 human, 166
 Malarial organisms, 396, 405, 409
 Mammals, intersexuality, 345
 Marshall, F. H. A., Sexual Physiology, 135
 Martin, R., Anthropometry, 127
 Masters, D., Conquest of Disease, 128
 MATTHEW, W. D., Evolution of the Horse, 139-185
 Maturation divisions, 419
 McDougall, W., Abnormal Psychology, 602
 Meek, C. K., Northern Tribes of Nigeria, 450
 Melin, E., Symbiotic Relation between Fungi and Roots, 598
Merychippus, 158
Mesobippus, 155
 Mesomorph, 361
 Meyer, A., Birth Control, 128
 Meyerhof, O., Chemical Dynamics of Life Phenomena, 134
 Michaelis, L., Ions in Colloidal Systems, 134
 Migration, plants, 214
 Minkowski, M., Reflex Activity, 137
Miohippus, 156
 Mitchell-Hedges, F. A., Battles with Giant Fish, 592
 Mitosis, amoeba, 109
 heterotypic, 421
 homeotypic, 421
 Monkeys, fetal growth, 477
 fetuses, 467
 MOORE, CARL R., Mammalian Testis and Scrotum, 4-50
 More, L. T., Evolution, 296
 Morgan, C. L., Life, Mind, and Spirit, 446
 MORGAN, T. H., Chromosomes and Genetics, 186-211
 Morgan, T. H., Evolution and Genetics, 296
 Theory of the Gene, 448, 578
 MORPHOLOGY (book reviews), 131, 306, 456, 599
 Morse, W., Applied Biochemistry, 460
 Much, H., Homeopathy, 464
 Nature of Disease, 128
 Müller, A., Philosophy of Biology, 587
 Murray, R. H., Science and Scientists, 313
 Myers, J. A., Vital Capacity of Lungs, 132
 Myerson, A., Inheritance of Mental Diseases, 125

- Nall, G. H., Sea Trout Scales, 455
 Needham, D. M., Brighter Biochemistry, 461
 Neurone, development, 62
 selectivity, 78
 Nervous system, hyperplasia, 63
 morphogenesis, 61
 proliferation of cells, 66
 regeneration, 81
 Newman, H. H., Evolution, Genetics and Eugenics, 296
 Gist of Evolution, 584
 Nicolai, G. F., Biology of War, 128
 Nordenskiöld, E., History of Biology, 586
- Oenothera*, genes, 287
 genetics, 283
 linkage, 287
 Renner's studies, 283
 Ontogeny, termites, 529
 Orang-utan, fetal growth, 477
Orobippus, 154
 Overstreet, H. A., Human Behavior, 310
- Paleontology, plants, 221
Parabippus, 156
Paramecium, asexual generations, 436
 drug-resistance, 258
 endomixis, 437
 Parasitism, aggressivity, 407
 carriers, 408
 definition, 393
 epidemiology, 395
 host susceptibility, 412
 immunology, 406
 infectivity, 413
 latency, 409
 pathogenesis, 405
 periods, 399
 relapse, 409
 specificity, 412
 symptomatology, 405
 therapeutics, 410
 Parasitism and symbiosis, 52
 Parasitological periods, 399
 Parker, G. H., Evolution, 124
 Parsons, T. B., Biochemistry, 133
 Pathogenesis, parasitism, 405
 Patten, C. J., Passing of the Phantoms, 447
 Pauchet, V., and Dupret, S., Pocket Anatomy, 456
 PAYNE, NELLIE M., Insects at Low Temperature, 270-282
 PEARL, RAYMOND, Cost of Biological Books in 1926, 606-608
 Biology of Population Growth, 300
 Foreword, 1-3
- Pearse, A. S., Animal Ecology, 591
 Pearson, W. A., and Hepburn, J. S., Physiological and Clinical Chemistry, 135
 Perrier, E., Evolution of Life, 125
 Petit, G., Male Genito-urinary Organs of Sirenians, 132
 Petitsclerc, P., Solitary Snipe, 593
 Pfeiffer, H., Experimental Morphology in Plants, 306
 Pfeiffer, Dr., Syphilis and Cancer, 590
 Philip, J. C., Physical Chemistry, 134
 Phillips, R. L., Vertebrate Embryology, 131
 Photoperiodism, 87
Phrynotettix magnus, 429
 Phylogeny, termites, 528
 PHYSIOLOGY (book reviews), 132, 307, 457, 599
 Plant breeding, 91
 Plant growth, 87
 Plants, age of endemics, 231
 antiquity and dispersal, 212
 paleontotology, 221
 ranges of endemics, 238
 rate of migration, 214
 Plants in lakes, 573
 Plants, low temperature, 270
 Plankton, 572
Plasippus, 162
 Plimmer, R. H. A., and Plimmer, V. G., Food and Health, 133
Pliobippus, 161
 Polya, G., and Riebesell, P., Biometry, 135
 Protozoa, man, 393
 termites, 53
 PSYCHOLOGY AND BEHAVIOR (book reviews), 137, 309, 462, 602
- Quercus*, 231
 Quevli, N., Enzyme Intelligence, 126
- Racc, black, 362
 white, 372
 yellow-brown, 366
 Recapitulation theory, 467
 Regeneration, ameba, 111
 nervous system, 81
 Relapse, parasitism, 409
 Rendle, A. B., Classification of Flowering Plants, 598
 Renner, O., Genetics in *Oenothera*, 299
 Oenothera, 283
 Resistance, host, 402
 parasite, 403
 passive, 402
 trypanosomes, 246
Reticulitermes flavipes, 55
 Retterer, E., Puberty and Sexual Maturity, 136
 Rhinoceros, 147, 166

- Rhinotermitidae, 544
 Richards, A., General Zoology, 305
 Rickey, E., Behavior of the White Rat, 310
 Roentgen rays, effects on testis, 29
 Röhm, G., Australian Totemism, 450
 Ross, J., Red Deer, 592
 Roussey, B., Anthropometry, 462
 Rowley, J., Taxidermy and Museum Exhibition, 454
- Sanger, M., International Aspects of Birth Control, 451
 Problems of Overpopulation, 451
 Sars, G. O., Crustacea of Norway, 593
 Schack, A. P., Evolution, 444
 SCHAEFFER, A. A., Biology of Ameba, 95-118
 Taxonomy of the Amebas, 454
 Scheidt, W., Anthropology, 303
 Schiller, F. C. S., Eugenics and Politics, 590
 Schmorl, G., Histological Methods in Pathology, 457
 Schoenichen, W., Plant Biology, 456
 SCHULTZ, ADOLPH H., Fetal Growth of Man and other Primates, 465-521
 Schulze, P., Biology of Animals in Germany, 299
 Scott, G. G. Biology, 125
 Scrotum, functional significance, 25, 27
 insulation, 26
 temperature, 25
 Sex (book reviews), 135, 461
 Sex chromosomes, flowering plants, 195
 Sex determination, chromosomes, 316
 Sex, lower plants, 200
 Sexuality, abnormal, 315
 animals, 315
 Shaw, H. L. K., The Child, 128
 Shearcroft, W. F. F., Matter, Man and Mind, 463
 Shelford, V. E., Naturalist's Guide to the Americas, 448
 Shull, A. F., Heredity, 447
 Silkworm, gynandromorphism, 327
 Simpson, J. Y., Science and Religion, 463
 Size and space, 221, 555
 Skramlik, E. von, Physiology of the Lower Senses, 600
 Smallwood, W. M., Biology, 126
 Smith, G. Elliott, Evolution of Man, 124
 Snodgrass, R. E., Honey Bee, 129
 SNYDER, THOMAS ELLIOTT, Biology of the Termite Castes, 522-552
 Sørensen, S. P. L., Proteins, 601
 Species, dispersal, 240
 Sporozoa, man, 395
 Spöttel, W., Inheritance in Wool, 297
 Starling, E. H., Human Physiology, 599
 Stempell, W., General Zoology, 304, 453
 Stevens, F. L., Plant Disease Fungi, 456
 Stiles, P. G., Human Physiology, 132
 Nutritional Physiology, 133
 Stiles, W., Photosynthesis, 131
 Stoermer, R., Oxidation and Reduction, 309
 Stolze, K. V., Chromosomes in Plants, 298
Stratoster, 564
 STURTEVANT, A. H., Genetics of *Oenothera*, 283-288
 Sweeney, J. S., Natural Increase of Mankind, 303
 Symbiosis, 51
 Symptomatology, parasitism, 405
 Synapsis, 425
- TALIAFERRO, WILLIAM H., Trypanosomiasis and Malaria, 246-269
 Tapir, 148, 166
 Taxonomy, termites, 526
 Temperature, low, animals, 273
 insects, 275
 plants, 270
 Temperature, scrotal and abdominal, 25
 Termites, 522
 castes, 524
 colonies, 541
 food, 53
 freeing from protozoa, 55
 nests, 541
 ontogeny, 529
 phylogeny, 528
 protozoa, 51
 taxonomy, 526
Termitidae, 547
 Terroine, E. F., and Zunz, E., Basal Metabolism, 133
 Testis, effects of alcohol, 32
 effects of dietary deficiencies, 33
 effects of roentgen rays, 29
 hypersensitive reactions, 31
 internal secretion, 34
 interstitial cells, 6, 37
 mammalian, 4
 seasonal cycle, 42
 Therapeutics, parasitism, 410
 Thom, C., and Church, M. B., Aspergilli, 598
 Thomas, S., Bacteriology, 130
 Thompson, I. M., Elements of Surface Anatomy, 457
 Thomson, J. A., Natural History, 585
 Thorburn, A., British Birds, 129, 304, 591
 Thornton, J., Human Physiology, 600
Tisanothera, 169
 Többen, H., Incest, 136
 Tocher, J. F., Variations in Milk, 309
 Transplantation, eye, 80
 limbs, 61
 testis, 19
 Trelease, W., American Oaks, 305

- Trichomonas hominis*, 396, 401, 403
 Trypanosomes, host resistance, 246
 lethal, 262
 mouse, 251
 non-lethal, 262
 non-pathogenic, 258
 pathogenic, 251
Trypanosoma gambiense, 253
 louis, 246, 406
 rhodesiense, 253
 Turck Foundation, Nature's Alchemy, 603

 Ubisch, G. von, Genetics of Heterostylism in Plants, 299

 Variability, fetuses, 507
 Varigny, H. de, Biology of Death, 586
 Vasectomy, 12
 Vavilov, N. I., Origin of Cultivated Plants, 597
 Vignes, H., Abortion and Sterility, 586
 Vincent, M., Hydrogen Ion Concentration, 135
 Voronoff, S., Rejuvenation by Grafting, 136

 Waite, H. H., Disease Prevention, 464
 Ward, A. R., and Gallagher, B. A., Diseases of Domesticated Birds, 594
 Wasmann, E., Mimicry in Ants, 305
 Watson, J. B., Behaviorism, 310
 Wattstein, F., von, Genetics of Mosses, 299
 Weaver, J. E., Root Development of Field Crops, 595
 Weinberg, M., Feminism, 128

 Wellensiek, S. J., Genetics of the Pea, 298
 Wells, H. G., Chemical Pathology, 460
 Wheeler, W. M., Watson on Behaviorism, 439-443
 Wheless, J., Is it God's Word?, 462
 White, W. A., Psychopathology, 129
 White ants, 523 (see Termites)
 Whitehead, A. N., Science and Modern World, 289
 Wiedemann, E., Growth of Trees in the Pine Forests of Saxony, 602
 Wilder, H. H., Pedigree of the Human Race, 451
 Willis, J. C., Age and Area, 553-571
 Winkelhagen, J., Birth Rate, 129
 Woodruff, LORANDE L., Asexual Reproduction in *Paramecium*, 436-438
 Woods, H., Invertebrate Paleontology, 594

 Yerkes, R. M., and Learned, B. W., Chimpanzee Intelligence, 137
 Yerkes, R. M., Psychology of Lower Primates, 137
 Y-chromosome, genes, 205
 Yorke, W., and Maplestone, P. A., Nematode Parasites of Vertebrates, 452
 Ysander, F., Human Thoracopagic Monsters, 457

 Zimmer, A., Homeopathy, 307
Zoochlorella, 52
 ZOOLOGY (book reviews), 129, 304, 451, 590
Zooxanthella, 52
 Zsigmondy, R., and Thiessen, P. A., Colloid Gold, 601

